Insecticide drift from agricultural spraying into field margin habitats and its effects on non-target arthropods:

residual toxicity, impact on populations, and recolonisation processes

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ZUSAMMENFASSUNG

Im Rahmen von Freilanduntersuchungen südlich von Hannover wurde die während der Applikation auf Weizenflächen auftretende Abdrift des Insektizids Trafo® (λ-cyhalothrin) in angrenzende, 3 m breite Ackerrandstreifen untersucht. Die Abdrift wurde anhand von Depositionsmessungen mit einem fluoreszierenden Farbstoff quantifiziert sowie ihre Auswirkungen auf Ziel- und Nichtzielarthropoden ermittelt. Driftbeläge auf Pflanzenoberflächen in 1, 2 und 3 m Entfernung vom Feldrand sowie Spritzbeläge auf im Feld exponierten Pflanzen wurden gemessen. Driftbeläge wurden bis zu 3 m Entfernung vom Feldrand nachgewiesen; sie zeigten eine hohe Variabilität. In Toxizitätsstudien wurden Indikatororganismen, *Aphidius colemani* Viereck (Hym., Braconidae) und *Coccinella septempunctata* L. (Col., Coccinellidae), den Insektizid-belägen auf Blattflächen ausgesetzt. Mindestens bis zu 3 m Entfernung vom Feldrand hatten die Driftbeläge eine toxische Wirkung gegenüber beiden Testorganismen.
Die Auswirkungen der Insektizidabdrift auf die Populationsdynamik von Blattläusen und ausgewählten Gruppen ihrer natürlichen Gegenspieler (räuberische Chrysopiden, Coccinelliden, Syrphiden sowie Blattlausparasitoide (Braconiden)) innerhalb der Ackerrandstreifen wurden untersucht. Signifikante Drifteffekte zeigten sich auf die Populationsdynamik von Blattläusen und Coccinelliden. Keine signifikanten Effekte wurden dagegen gegenüber verschiedenen Entwicklungsstadien von Chrysopiden, Syrphiden und Blattlausparasitoiden festgestellt. Nach der Insektizidbehandlung wurde die Erholung von Populationen, durch Reproduktion bzw. Wiederbesiedlung, in Weizenbereichen neben Drift-geschützten und Drift-kontaminierten Ackerrandstreifen analysiert. Drift-geschützte, nicht aber Drift-kontaminierte, Randstreifen hatten einen positiven Effekt auf Blattlausdichten im Weizen im Abstand von 4 bzw. 5 m vom Feldrand. Eine Einwanderung von Coccinelliden und adulten Syrphiden aus beiden Randstreifentypen in dicht an sie angrenzende Weizenbereiche zeichnete sich ab.
Um das Wiederbesiedlungspotential von Blattlausparasitoiden aus Ackerrandstrukturen heraus zu analysieren wurden Dispersionsstudien mit zwei *Aphidius*-Arten durchgeführt. In der ersten Studie wurde das Ausbreitungsverhalten von freigesetzten Parasitoiden anhand der Parasitierung von Blattläusen auf Fangpflanzen analysiert. In der zweiten Studie wurde eine Protein-Markierungs-Wiederfang-Methode angewendet. Beide Untersuchungen zeigten die sofortige Ausbreitung der Parasitoide nach ihrer Freilassung; innerhalb von 48 Stunden legten sie mindestens eine Entfernung 16 bzw. 48 m vom Freilassungspunkt zurück.

Schlagworte: Driftdeposition, Ackerrandstreifen, Wiederbesiedlung

ABSTRACT

Within the scope of this thesis drift of the pyrethroid Trafo® (λ-cyhalothrin) into 3 m wide field margin strips running alongside conventionally managed winter wheat fields in Lower Saxony, Germany, and its effects on target and non-target arthropods was investigated. Drift deposition on off-crop plant surfaces at 1, 2, and 3 m from the field edge as well as spray deposition on within-field plants was quantified using a fluorescent tracer. Insecticide application in the wheat crop resulted in patchy drift deposition on off-crop plant surfaces up to 3 m from the field edge. The toxicity of insecticide deposits on leaf surfaces to two indicator organisms, adult *Aphidius colemani* Viereck (Hym., Braconidae) and *Coccinella septempunctata* L. (Col., Coccinellidae) larvae, was estimated. Both test organisms were affected by drift at least up to a distance of 3 m from the sprayed crop.

The effects of λ-cyhalothrin drift on the population dynamics of aphids and selected groups of their natural enemies, i.e. plant dwelling predators of the families Coccinellidae, Chrysopidae, and Syrphidae, and cereal aphid parasitoids of the family Braconidae, within the field margin strips were evaluated. Drift of λ-cyhalothrin into the field margins significantly affected the population dynamics of aphids and coccinellids, whereas no significant drift effects on developmental stages of chrysopids, syrphids, and aphid parasitoids were detected. An analysis of reimmigration/reproduction-mediated recovery of populations in wheat areas adjacent to drift-contaminated and drift-protected field margins was carried out. Drift-protected, but not drift-contaminated, field margins had a promoting effect on aphid densities at 4 and 5 m, respectively, into the wheat. Furthermore, field observations indicated an immigration of syrphid flies and coccinellids, respectively, from both drift-protected and drift-contaminated field margins into closely adjoining wheat areas.

To estimate the reimmigration potential of aphid parasitoids from field margins into crops, dispersal studies with two *Aphidius* species were conducted. The first study assessed the dispersal of released female parasitoids on the basis of mummified aphids on trap plants, whereas the second study used protein-marking (rabbit immunoglobulin G) and recapture. Results indicated that parasitoids tend to disperse after release. In both studies parasitoids moved to the farthest distance from the release points at which dispersal was estimated (i.e. 16 and 48 m, respectively) within less than 48 hours.

Keywords: insecticide drift deposition, field margin, recolonisation

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1. GENERAL INTRODUCTION

Since the 1940s there has been a great increase in the intensification and industrialisation of agriculture in Germany as well as in most European countries (e.g. Björklund, 1999; Kühne & Freier, 2001; Robinson & Sutherland, 2002; EEA, 2003; Hutton & Giller, 2003). Based on the belief that food demand would increase faster than food production (Torres et al., 2000), farmers were urged to increase their output. The intensification was largely supported and enforced by government policies in both western and eastern European countries (Kühne & Freier, 2001; Prazan, 2002). The transformation into this "modern" form of agriculture was connected with technological advances that entailed the replacement of traditional practices by high-input farming (including heavy use of synthetic fertilisers and pesticides, monocropping, intensive tillage, or intense irrigation) (Björklund, 1999; Prazan, 2002). Moreover, the former small-scale mosaic landscape that was characterised by a high diversity of habitat types, such as small arable fields and pastures, wetlands, hedges, groves, and field margins had undergone a radical modification since the change in land use was associated with the conversion of grasslands into arable land, the destruction of woodlots, the drainage of wet meadows and ditches, and the removal of field margins and hedgerows in favour of increasing field sizes (e.g. Björklund, 1999; Kühne & Freier, 2001; Robinson & Sutherland, 2002; EEA, 2003; Waldhardt et al., 2003). This consolidation of arable land resulted in highly managed monoculture landscapes with reduced and fragmented habitat patches. In 2002, more than 50 % of the total European area and 47.5 % of the total area of Germany, respectively, was devoted to agriculture (FAO, 2004).

The intensification of agricultural practices and the loss of (semi-) natural habitat types from the landscape have been shown to have a negative impact on species diversity, in particular diversity of taxa associated with farmland (e.g. Nentwig, 2000a; Robinson & Sutherland, 2002). An overall severe decline in the diversity of plant species on arable land and in field boundaries was observed (Boutin & Jobin, 1998; Altieri, 1999; Waldhartdt et al., 2003). Although only limited data from long-term monitoring studies are available (Robinson & Sutherland, 2002), agricultural intensification is supposed to have caused a large decline in a range of invertebrate species, for example in butterflies, carabids, grasshoppers, dragonflies, or bumblebees (e.g. Warren et al., 2001; Kells et al., 2001; Robinson & Sutherland, 2002). Long-term monitoring studies from Great Britain have shown that industrial agriculture caused a large decrease in farmland bird populations, e.g. due to a loss of breeding sites or depletion of food resources (Chamberlain et al., 2000; Donald et al., 2002; EEA, 2002). Many species

from other vertebrate classes (mammals, reptiles, and amphibians) are also thought to be impaired by agricultural intensification (Robinson & Sutherland, 2002).
However, not all organisms are negatively affected by the intensive agriculture. Many habitat generalists are still common on agricultural land, for example the generalist arthropod predators *Erigone atra* Blackwall (Linyphiidae) or *Pterostichus melanarius* (Illig.) (Carabidae) (Sunderland, 1987; Kromp, 1989; Robinson & Sutherland, 2002; Belaoussoff et al., 2003). These species are preadapted to disturbed and ephemeral habitats (Wise, 1993; Ribera et al., 2001). But habitat specialists or species with low mobility were found to be in decline in patchy landscapes, for instance several butterfly species (Warren et al., 2001; Brereton, 2004). The main reasons for the declines in many species are the decrease in habitat features (e.g. loss of feeding or breeding sites for species reliant on certain host plants or plant communities), the isolation of the remaining habitat patches, and the extensive use of pesticides. In particular insecticides often do not only affect the target pests but also non-target invertebrate groups. Thus, their use can have devastating effects on the food-chain of faunal groups of arable land (e.g. Holland et al., 1999; Moreby et al., 2001) and, furthermore, insecticide treatments can deplete natural enemy abundances, thereby disrupting biological pest control (Duffield & Aebischer, 1994).

Because of the reduced availability of natural habitats in the agricultural environment, field margins have become key features in today's agricultural landscapes (Denys & Tscharntke, 2002; Marshall & Moonen, 2002). Field margin habitats are linear structures that form the border of agricultural fields. These habitat types are usually 1 m to a few metres wide and can form networks of several thousands of kilometres (Welling, 1987; Kühne et al., 2000; Helenius & Bäckman, 2004). Therefore they can act as corridors for the movement of animals between crops as well as between crop and off-crop (Good, 1998; Marshall & Moonen, 2002). In contrast to the large monoculture fields, these semi-natural habitats are characterised by a more diverse vegetation, e.g. plant communities typical of arable land or disturbed ground as well as communities of other adjacent habitats (Marshall & Moonen, 2002). In recent times the value of field margins for arthropods but also vertebrates (e.g. birds) was increased by the establishment of wild flower margins, using seed mixtures especially designed for the attraction of a variety of beneficial arthropod species (e.g. Nentwig, 1992; Nentwig, 2000b; Marshall & Moonen, 2002; Boller et al., 2004; Marshall, 2004).
In recent years there has been a reorientation of the agricultural policy in the European Union. Financial support resulted for example in an increase in organic farming during the past ten years or in restoration of habitats in the agricultural landscape (Lampkin et

al., 1999; EEA, 2002). Since 2004, the establishment of flowering field margins along agricultural fields in Germany is financially supported by the government and the EU (anonymous, 2004), thereby expanding former regional support measures.

Field margins, either sown or “natural”, serve important functions for different arthropod groups typical for agroecosystems. They support alternative food or hosts for important natural enemies of crop pests, such as soil and plant dwelling predators, e.g. ground beetles (Carabidae), ladybeetles (Coccinellidae), lacewing (Chrysopidae) and hoverfly (Syrphidae) larvae, and spiders (Araneae) as well as aphid parasitoids (e.g. Frank, 1999; Lee, 2001; Marshall & Moonen, 2002; Langer & Hance, 2004). As a result, these habitats are thought to have an important function for pest regulation in the adjacent crops. Furthermore, margin strips with a high density of flowers have been shown to enhance insect species that depend on nectar and pollen as food, such as hoverflies, different Hymenopterans, or butterflies (Frank, 1999; MacLeod, 1999; Warren et al., 2001; Kells et al., 2001; Sigsgaard, 2002; Boller et al., 2004). For predominantly field inhabiting groups, like carabid beetles or certain spider species, field margins can be temporary refuges during and after harvest or tillage or act as overwintering sites from which movement into the adjoining crop occurs in spring (Purvis & Fadl, 1996; Varchola & Dunn, 2001; Lemke & Poehling, 2002; Frank & Reichhart, 2004; MacLeod et al., 2004). Furthermore, field margin habitats can harbour source populations that possibly contribute to repopulation of insecticide depleted fields (e.g. Duffield et al., 1996; Longley et al., 1997a; Holland et al., 1999; Holland et al., 2000; Lee et al., 2001). Thus, the close vicinity of the field margin habitat to the arable field can have a positive effect on the within-field pest regulation. Contrariwise, field margins are endangered due to their close proximity to agricultural actions, such as the application of pesticides, which can have detrimental impacts on field margin flora and fauna. The application of plant protection products is generally associated with the occurrence of direct drift (Kaul et al., 2001a,b), i.e. the movement of pesticide droplets from the intended area of application to non-target areas during the application. Drift is considered to be the most relevant route of contamination of terrestrial off-crop areas (Candolfi et al., 2001; Koch et al., 2003). The level of drift deposition into field margins depends on meteorological conditions while spraying (e.g. wind speed and direction) and technical features such as droplet spectrum, distance of nozzles to target area, travel speed, and application rate (Thistle et al., 1998; Kaul et al., 2001a; Koch et al., 2003).

The EU Council Directive 91/414/EEC (EEC, 2004) concerning the placing of plant protection products on the market, which has already been transposed into German law, demands that plant protection products that are used as prescribed shall not

cause unacceptable effects on the environment and on non-target species. This demand does not only include in-field risks, but also risks for non-target (arthropod) populations in off-crop habitats that may arise from insecticide drift (anonymous, 2003a). To reduce pesticide drift deposition into field margin habitats, spray drift mitigation strategies have been established. In Germany, the application of most plant protection products is regulated by sanctions that dictate buffer zone distances (between 5 and 20 m) to terrestrial off-crop habitats while spraying and/or the use of drift reducing techniques (BBA, 2002a). However, since these requirements are softened by many exceptions (e.g. they do not apply to habitats that are less than 3 m wide (BVL, 2003)), they do not guarantee absolute protection of non-target areas. Furthermore, the compliance with regulations by farmers cannot be assured.

The Council Directive 91/414/EEC requires plant protection product registrants to reliably assess potential environmental risks of their products to non-target organisms. The ecological risk assessment relies on a tiered testing system with clearly defined protocols (e.g. Barrett et al., 1994; Candolfi et al. 2000a, 2001). However, to date there are still significant gaps in the exposure assessment for terrestrial non-target arthropods due to pesticide drift (Gonzales-Valero et al., 2000; Candolfi et al., 2001; Candolfi, personal communication). In the current risk assessment procedures the potential off-field hazards for non-target arthropods are calculated from application rates, LR_{50} values from laboratory testing and available spray drift data (German spray drift model, Ganzelmeier et al., 1995). Since the latter are based on drift measurements on two-dimensional horizontal surfaces, a “vegetation distribution factor” is used to account for the three-dimensional terrestrial habitat (Gonzales-Valero, 2000; Candolfi et al., 2001). However, this theoretical estimation of spray drift has been criticised due to its lack of realism and has led to the demand for the measurement of spray drift deposition into plant canopies in order to achieve realistic three-dimensional spray drift data (e.g. Gonzales-Valero, 2000; Koch & Weißer, 2004). First data from such measurements are available (e.g. Koch & Weißer, 2004; Koch et al., 2004a; this study) and may be used for an improvement of the exposure assessment for terrestrial non-target arthropods in off-crop areas (Candolfi, personal communication). The first part of the present work depicts results from quantitative insecticide drift deposit measurements on plant surfaces in a complex field margin habitat. The test substance was the broad-spectrum pyrethroid λ–cyhalothrin, which is one of the most widely used insecticides in Europe (anonymous, 2000a; Kühne et al., 2002). The toxicity of λ-cyhalothrin drift deposits was estimated in an exposure bioassay using two important natural enemies of aphids, a parasitoid and a coccinellid species, as indicator organisms.

So far, the availability of published data from field studies regarding insecticide drift into field margins and the associated risks for populations of non-target arthropods is limited. Kühne et al. (2002) determined insecticide (λ-cyhalothrin) drift into a grassy field margin and analysed the effects on arthropod populations. They concluded that spray drift may primarily be harmful to arthropods close (i.e. 1 m) to the field edge. Overall, the study did not detect effects on a large number of different arthropod groups and species under investigation. But for few organisms that are highly sensitive to λ-cyhalothrin (e.g. mites and coccinellids) potential risks could not be excluded up to a distance of 5 m from the field edge. Although the estimation of drift effects was not the primary research question, two other studies provide useful information on effects of insecticide drift on non-target arthropods. Holland et al. (1999 & 2000) showed that insecticide (dimethoate) drift caused a significant decline in aphid parasitoid, spider (Linyphiidae), and total arthropod numbers within a 6 m wide unsprayed buffer zone. The second part of the current study elucidated the effects of λ-cyhalothrin drift into a 3 m broad field margin strip on population dynamics of selected groups of natural enemies of aphids. The post-treatment recovery of insect populations in adjacent wheat fields through reproduction and immigration from field margins was investigated.

Several studies found evidence for the recolonisation of insecticide treated wheat fields by carabid beetles from undisturbed surrounding habitats (e.g. Duffield & Aebischer, 1994; Holland & Luff, 2000; Holland et al., 2000) and spiders from within-crop sown weed strips (Lemke, 1999). So far, the possible reimmigration of another important group of natural enemies, the aphid parasitoids, has rarely been investigated in detail. Longley et al. (1997a) suggested that population recovery of aphid parasitoids within an insecticide-treated wheat field was mainly due to immigration of parasitoids from untreated surrounding habitats. However, they did not locate the source of immigrating wasps. A major obstacle to understanding the reinvasion-mediated recovery of parasitoid populations following pesticide treatments is the limited information that is available on aphid parasitoid dispersal under field conditions. Evidence is needed that parasitoids are able (and “willing”) to move between habitats, which is a prerequisite for the recolonisation of crops from surrounding sources (Lavandero et al., 2004). The analysis of parasitoid movement in the field requires an appropriate experimental design, which often involves marking, release into the field and the subsequent recapture of marked specimens at different spatial and temporal intervals (Hagler & Jackson, 2001; Lavandero et al., 2004). Numerous methodologies have been used so far to investigate the field dispersal of hymenopterans (e.g. Corbett & Rosenheim, 1996; Fernandes et al., 1997; Hagler et al., 2002a,b; Desouhant et al., 2003;

Schellhorn et al., 2004). However, each approach has its limitations (e.g. labour and time intensiveness, side-effects of markers, expensiveness) and may be appropriate for dispersal studies with a certain species but inappropriate for another. Thus, the third and the fourth part of the current work investigated the dispersal capability of two aphid parasitoid species using two different methodological approaches. In the first dispersal study the marking of parasitoids was avoided by using a non-native species; parasitoid movement was estimated on the basis of mummified aphids on trap plants deployed at different distances from a central release point. In the second dispersal study a mark-release-recapture technique, using protein-marking, was used to investigate the immigration of parasitoids from the field margin into an adjacent wheat field. The results obtained by both studies can help to reduce the lack of knowledge in aphid parasitoid dispersal and their potential to reinvade into crop fields subsequent to insecticide applications.

The objectives of the present work were:

(1) to quantify λ-cyhalothrin drift into field margins by measuring drift deposition on plant surfaces and to analyse the effect of drift deposits on two beneficial non-target arthropods, *Aphidius colemani* Viereck (Hymenoptera: Braconidae) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae),

(2) to estimate the effects of λ-cyhalothrin drift into field margin habitats on population dynamics of aphids and selected groups of their natural enemies (i.e. chrysopids, coccinellids, aphid parasitoids, and syrphids) and to investigate the post-treatment recovery of insect populations in adjacent wheat fields through reproduction and reimmigration from drift-protected and drift-contaminated field margins,

(3) to analyse the initial dispersal of the aphid parasitoid *A. colemani* by means of aphid infested trap plants in order to estimate its potential to contribute to recolonisation processes into insecticide treated crops, and

(4) to investigate the immigration of the cereal aphid parasitoid *Aphidius rhopalosiphi* DeStefani-Perez (Hymenoptera: Braconidae) from field margins into λ-cyhalothrin treated wheat fields using mark-release-recapture studies.

2. *Insecticide drift deposition on off-crop plant surfaces and its impact on two beneficial non-target arthropods,* **Aphidius colemani** *Viereck (Hymenoptera: Braconidae) and* **Coccinella septempunctata** *L. (Coleoptera: Coccinellidae)**

2.1 INTRODUCTION

The application of plant protection products is generally associated with the occurrence of direct drift (Kaul et al., 2001a), i.e. the movement of pesticide droplets from the intended area of application to non-target off-crop areas during the application caused by air movements (Ganzelmeier et al., 1995). Direct drift is a complex process, which is influenced by technical conditions (e.g. droplet spectrum, distance of nozzles to target area, travel speed, and application rate) and prevailing meteorological conditions (e.g. wind speed and direction, psychometric temperature difference of the air) (Thistle et al., 1998; Kaul et al., 2001a; Koch et al., 2003). Due to their close proximity to agricultural operations field margin habitats can be adversely affected by pesticide spray drift during insecticide application, which is considered to be the most relevant route of contamination of terrestrial off-crop areas (Candolfi et al., 2001; Koch et al., 2003). Risks for off-crop areas, particularly field margin habitats, demand attention, since in intensively managed agricultural landscapes these habitats enjoy important environmental and conservation functions. They can be refuges for many plant species and support a diverse fauna, including mammals, birds, and invertebrates (Marshall & Moonen, 2002). Many studies have shown the value of well-structured field boundary habitats for the increase of population densities of different arthropod species typical for agro-ecosystems (e.g. MacLeod, 1999; Thomas & Marshall, 1999; Sutherland et al., 2001a). For natural enemies of insect pests, such as parasitoids and generalist predators, field margins can be permanent habitats but can also act as corridors for the movement between crop and off-crop (Joyce et al., 1999; Marshall & Moonen, 2002). By offering alternative prey or hosts field margins can offer temporary refuges after harvest or tillage and act as overwintering sites for a variety of arthropod species (Landis et al., 2000; Varchola & Dunn, 2001; Lemke & Poehling, 2002). They can also harbour source populations and contribute to the recolonisation of insecticide treated fields (Nachtigall, 1994; Longley et al., 1997a). By preserving and supporting beneficial arthropod fauna field margin habitats may contribute to the reduction of pest outbreaks in arable field crops (Landis et al., 2000; Denys & Tscharntke, 2002). Consequently, it is an important aim of long term sustainable plant protection strategies to prevent risks,

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such as insecticide spray drift, from these natural and semi-natural habitats adjacent to arable fields.

Until now, very few field studies have investigated the effects of pesticide drift on non-target arthropods within terrestrial habitats. By connecting λ-cyhalothrin spray drift deposition pattern within a 5 m wide field margin strip with mortality data from laboratory testings, Kühne et al. (2002) showed that drift depositions may cause mortality > 50 % to the predatory mite *Typhlodromus pyri* Scheuten (Phytoseiidae) at any position within the strip; risks for adult seven-spotted ladybeetles, *Coccinella septempunctata* L. (Coccinellidae), were slightly lower. For other indicator organisms, being less susceptible to λ-cyhalothrin (e.g. larvae of the lacewing *Chrysoperla carnea* Stephens (Chrysopidae), adult wolf spiders of the genus *Pardosa* spp. (Lycosidae), and adults of the carabid beetle *Poecilus cupreus* L. (Carabidae)) lower risks were predicted. Earlier studies directly estimated spray drift effects on indicator species using bioassays; for example Davis et al. (1993) examined effects of insecticide (cypermethrin) drift on larvae of the Large Cabbage White Butterfly, *Pieris brassicae* L. (Pieridae). Depending on meteorological conditions during the application, mortality levels of 50 % were predicted up to 22.5 m downwind of the sprayed crop. Drift of the insecticide methomyl caused more than 70 % mortality to the aphid parasitoid *Aphidius colemani* Viereck (Braconidae) exposed to plant surfaces at 0.6 m and 2 m downwind from the sprayed crop (Langhof et al., 2003).

Kühne et al. (2002) investigated effects of insecticide drift on distribution pattern of selected arthropod groups; they found significant reductions in numbers of mites and grasshoppers as well as total numbers of arthropods caused by λ-cyhalothrin drift into a field margin habitat. Densities of all other arthropod groups under investigation were not reduced by the insecticide drift.

The current study investigates drift of the broad-spectrum pyrethroid Trafo® (active ingredient λ-cyhalothrin) into field margin habitats running alongside winter wheat fields and the toxicity of deposits to non-target arthropods. In addition to its novelty, this approach permits to elucidate drift deposit measurements on plant surfaces in a complex field margin habitat and to estimate the toxicity of these deposits to non-target arthropods. Lambda-cyhalothrin is one of the most widely used insecticides in Europe (anonymous, 2000a; Kühne et al., 2002) and was therefore chosen as test substance. In this study drift effects were estimated on adults of the aphid parasitoid *A. colemani* and larvae of the seven-spotted ladybeetle *C. septempunctata*. These test organisms were considered as representatives of the functional groups parasitoids and plant dwelling predators as abiding by the international guidelines on testing procedures for

effects of pesticides on non-target arthropods (Barrett et al., 1994). In addition, *C. septempunctata* and *Aphidius*-species are frequently found in typical grassy off-crop habitats of intensively managed central European agricultural landscapes (Roß-Nickoll et al., 2004). As an alternative of the standard test-species, *Aphidius rhopalosiphi* DeStefani-Perez, *A. colemani* was chosen due to its comparably high sensitivity towards insecticides (Maise et al., 1996), its affordable price, and wider availability from commercial suppliers.

There were two main objectives of the current work. The first was to measure insecticide drift deposits on plant surfaces in a complex field margin habitat. The second was to estimate the toxicity of these drift deposits to two non-target arthropod species. Data generated from a two-years field study.

Definitions

The term “within-crop” refers to the whole cropped area, i.e. the wheat crop, and “off-crop” defines the area outside the crop. The “field edge” is the boundary line between the within-crop area and the off-crop area.

2.2 MATERIAL AND METHODS

2.2.1 Experimental design

The study was carried out on three intensively farmed privately owned winter wheat fields 25 km south of Hannover, Germany. Parallel to the lane (i.e. the driving direction of the field sprayer) 3 m broad sown field margin strips, sown with a wild flower mixture (modified according to Nentwig, 1992; cf. 3.2.1, page 38), were established along one edge of each wheat field. Length of field margin strip 1 bordering on field 1 was 230 m, length of strip 2 bordering on field 2 was 234 m and length of strip 3 bordering on field 3 was 419 m. In order to provoke drift, detectable wind should preferably blow at an angle of 90° to the sown weed strips during insecticide application. Since strips 1 & 2 were west facing and strip 3 was south facing, in each year insecticide application to wheat fields 1 & 2 was performed on the same day and application to field 3 on a separate day. Field margin strips were divided into 16 plots of equal size (approximately 54 m), providing four experimental plots each on strips 1 & 2 and eight plots on strip 3 (cf. page 39).

2.2.2 Insecticide application

In both years the synthetic pyrethroid Trafo® (active ingredient λ-cyhalothrin) was applied at its respective recommended rate (2002, Trafo liquid, Urania: 10 g a.i./ha; 2003, Trafo WG, Syngenta: 7.5 g a.i./ha). The insecticide was applied at the middle/end of wheat flowering (BBCH 65/69) on 14 June (field 1 & 2) and 16 June (field 3) in 2002 and on 20 June (field 3) and 21 June (field 1 & 2) in 2003. Applications were done using a conventional tractor mounted field sprayer (15 m boom) equipped with multirange flat spray nozzles LU 120 03 (Lechler, Metzingen, Germany), i.e. a standard, non low-drift nozzle type. Nozzle spacing was 50 cm and boom height above the canopy was 50 cm. A spray volume of 200 l/ha was achieved with an operating pressure of 3.6 bar and a forward speed of 7.2 km/h (2002) and 3 bar and 6.4 km/h (2003), respectively. When operated at these pressure settings the nozzles produced approximately 10 to 15 % fine droplets (< 100 µm). A control and a drift-treatment were performed; these were randomly distributed among the 16 field margin plots. During insecticide application control weed strips were covered with polythene sheets to prevent contamination due to insecticide drift, whereas drift weed strips were left uncovered. Each treatment was replicated eight times. Wind speed and wind direction at the time of spraying were recorded at 2 m height at the experimental site using a stationary anemometer (Lambrecht, Göttingen, Germany) and a portable hand wind gauge (ELV Elektronik, Leer, Germany). Data on temperature and humidity were retrieved from a nearby (1 km) weather station at the Ruthe field station of the University of Hannover.

2.2.3 Spray drift deposit measurement

Spray drift deposits on plant surfaces were quantified following the method of Koch & Spieles (1992). The fluorescent tracer sodium fluorescein (Roth, Karlsruhe, Germany) was added to the spray liquid at a rate of 50 g/ha. Broad beans (*Vicia faba* L.) were used as spray drift collectors. Due to its relatively fast growth and its stable and large leaves, allowing both the measurement of drift deposits and the attachment of clip cages for the exposure bioassay, (see below), *V. faba* was found to be a suitable spray drift collector plant. Just prior to the application, potted plants were deployed in the sown weed strips at distances of 1, 2, and 3 m from the field edge and directly within the wheat field (2 m from the field edge), i.e. the latter bean plants were directly treated and therefore collected no drift deposits but spray deposits (Fig. 1). Pots were sunk

flush into the ground and height of bean plants corresponded approximately to the canopy height. In 2002 two bean plants were arranged side by side at each distance, one was exploited for the drift deposit measurement and the other for the exposure bioassay using *A. colemani* as target. In 2003 three bean plants were set up, the additional plant was devoted to the exposure bioassay with *C. septempunctata* larvae (see below). Within each weed strip plot, at each distance, three replications of plants were used in the drift treatment and two replications of plants were used in the control treatment (Fig. 1). Following post-application of the insecticide-tracer mixture, two leaves of each bean plant were cut off at the top of the canopy and at the ground level. Leaves were put into brown light-impervious 100 ml-plastic bottles and stored overnight in a cold storage room. The next day the tracer was washed off the leaves with tap water. The emission of the washing liquid was measured in a Perkin-Elmer LS-3 fluorescence spectrometer (Perkin-Elmer, Rodgau, Germany) at 484 nm and 512 nm excitation and emission wavelengths, respectively. After the size of the leaves was measured (using Bonit 1.0, LemnaTec, Würselen, Germany) the deposit of the insecticide in ng per cm² leaf surface was calculated. To compensate for disturbances by impurities (e.g. dust) on leaf surfaces, the mean fluorescence of “zero control” leaves, i.e. leaves that were sampled immediately prior to the insecticide-tracer application, was subtracted from each post-spray sample. The limit of detection for each trial was determined by multiplying the standard deviation of the zero control measurements by 3.3. For statistical analysis, measurements below detection limit were set to 0.

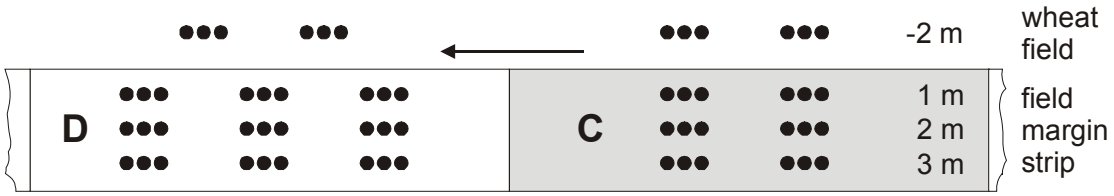

Fig. 1. Sketch (not to scale) showing positions of spray collector plants (black spots) in the wheat field and spray drift collector plants in the field margin strips of drift-treatment (D) and control (C). At each position one plant was used for the deposit measurement, one for the bioassay with *A. colemani* and, in 2003, one for the bioassay with *C. septempunctata* larvae. The arrowhead indicates the driving direction of the field sprayer.

2.2.4 Exposure bioassays

The toxicity of off-crop as well as within-crop deposits to adult *A. colemani* and *C. septempunctata* larvae was measured in an exposure bioassay in which test-organisms were exposed to dried insecticide deposits on plant surfaces. Therefore drift collecting bean plants were arranged in the way described above (Fig. 1). Right after the insecticide application, plants were taken to the laboratory and the clip cages enclosing the test-organisms were attached to the adaxial leaf-surface of the plants. The leaf area enclosed by a clip cage was 7.5 cm^2. Initial exposure of test organisms to insecticide deposits started four to eight hours after field application. The delayed exposure was owing to the time required in the field for the collection of leaves for the deposit measurement, the removal of bean plants from the field, and the return transport to the laboratory.

Exposure bioassay A. colemani

The exposure bioassay using *A. colemani* was conducted in years 2002 and 2003. One clip cage containing five adult *A. colemani* was attached to the adaxial surface of a leaf from the top of the canopy (herein after referred to as top-leaf) and a leaf from ground level (herein after referred to as bottom-leaf), respectively, of each plant. The parasitoids were supplied with small pieces of cotton wool soaked with water and honey. Both healthy (i.e. no crippled wings, no uncoordinated movements) males and females were used and selected impartially, i.e. without reference to their size, as abiding by Mead-Briggs et al. (2000). Plants with clip cages were stored in a climate chamber at 20°C, 60 % RH and a photoperiod of 16:8 h (L:D). Parasitoid mortality was investigated 12 and 24 hours after exposure of the insects to the leaves. *A. colemani* were supplied by a commercial supplier (Katz Biotech, Baruth, Germany).

***Exposure bioassay* C. septempunctata**

The exposure bioassay with *C. septempunctata* was conducted in 2003. To prevent cannibalism, L2-L3 *C. septempunctata* larvae were secluded each in a clip cage. Only toxicity of top-leaves was measured as described above. *C. septempunctata* larvae were daily offered ample amounts of *Aphis fabae* Scopoli (Aphididae). Plants with clip cages were stored in a climate chamber at a temperature of 22°C, 60 % RH and a photophase of 16:8 h (L:D). Mortality of larvae was assessed at three, 12, and 24 hours after exposure. *C. septempunctata* larvae used in the bioassay were laboratory-bred according to Samsoe-Petersen et al. (1989) and Hindayana (2001).

2.2.5 Data analysis

Differences in spray and spray drift deposits on leaves at different distances from the sprayed crop were elucidated by nonparametric Anova-type statistic (ATS) (Brunner & Munzel, 2002). Using Bonferroni correction, the alpha level (0.05) was adjusted to 0.0083 to compensate for multiple comparisons. The Wilcoxon signed-rank test for two related samples was performed to analyse differences in deposits on top- and bottom-leaves at the same distance. Exact p-values were computed via data permutation. Due to different meteorological conditions during the insecticide applications (see below), data analysis was done separately for each application date.

ATS was also performed to show differences in control-corrected mortalities (Schneider-Orelli, 1947) of *A. colemani* 12 and 24 hours after exposure and of *C. septempunctata* 3, 12, and 24 hours after exposure to spray deposits at different distances from the field edge. Using Bonferroni correction, the alpha level was lowered from 0.05 to 0.0083 to compensate for multiple comparisons. The Wilcoxon signed-rank test for two related samples was performed to analyse differences in control-corrected mortalities of *A. colemani* exposed to deposits on top- and bottom-leaves at the same distance. Exact p-values were computed via data permutation.

The relationship between the insecticide deposits measured on a bean leaf and the mortality of test organisms exposed for a period of 3, 12, and 24 hours, respectively, to deposits on a closely adjoining bean leaf was analysed using nonparametric bivariate correlation. Spearman's rank correlation coefficient, r_s, was computed, which is a measure of the correlation of both test variables. The correlation coefficient can range from -1 (complete discordance, negative correlation) to +1 (complete concordance, positive correlation) (Sachs, 2002). The absolute value of r_s indicates the strength of the relationship, with larger values indicating stronger relationships.

Data analysis was done using the programme SAS version 8.02 (SAS, 2001).

2.3 RESULTS

2.3.1 Meteorological data during application

Table 1 summarises data on wind speed and direction, temperature, and relative humidity recorded during the insecticide applications in 2002 and 2003. During none of the applications wind blew at the preferred angle of 90° to the weed strips. Except for a small amount of rain that fell approximately one hour after the application to field 3

(2002), no rainfall was recorded during a period of at least 12 hours subsequent to applications.

Tab. 1. Meteorological conditions during insecticide applications to wheat fields 1, 2, and 3 in 2002 and 2003.

Year	Field	Wind speed [m/s]			Mean wind direction towards field margin [°]	Temperature [°C]	RH [%]
		mean	min.	max.			
2002	1&2	0.5	0	1	10	20	77
2002	3	3.7	2.7	4.6	60	19	76
2003	1&2	4.1	1.1	6.1	53	18	55
2003	3	6.3	3.5	7	-10	18	54

2.3.2 Spray drift deposits on plant surfaces

Figures 2 to 5 show deposits of λ-cyhalothrin on individual leaves of broad bean plants within the crop (2 m from the field edge) and in the off-crop field margin strips at distances of 1, 2, and 3 m from the field edge. Table 2 lists deposit means and standard errors for different distances. In spite of different meteorological conditions during the four applications (Tab. 1), some overall patterns of deposition can be traced. Spray deposits on top-leaves from within-crop were always significantly higher compared to deposits on bottom-leaves from the same sample position (Fig. 2 to 5, Tab. A1, appendix). In addition, drift deposits on top-leaves at 1, 2, and 3 m distance from the field edge were always significantly lower compared to spray deposits on within-crop top-leaves (Fig. 2 to 5, Tab. A1, appendix). Deposits on within-crop bottom-leaves did not differ significantly from deposits on bottom-leaves at 1 m, but both were significantly higher compared to deposits at 2 and 3 m distance from the field edge (Fig. 2 to 5), except for insecticide application to field 3 in 2003, which produced a significantly different pattern of deposits on bottom-leaves (see below and Fig. 5, Tab. A1, appendix). Generally, insecticide applications produced highly variable deposits on individual leaves taken from collector plants that had been exposed at the same distance from the field edge (Fig. 2 to 5).

Deposits on top-leaves produced by insecticide application to fields 1 and 2 in 2002 significantly decreased with increasing distance from the field edge (Fig. 2, Tab. 2 and

A1, appendix). Low wind speed during insecticide application (Tab. 1) resulted in leaf samples with no drift deposits, i.e. measurements that were below detection level. On top-leaves at 2 and 3 m from the field edge 25 % and 38 %, respectively, of measurements were below detection level (Fig. 2). Deposits on bottom-leaves within-crop did not differ from bottom-leaf deposits at 1 m, but both were significantly higher compared to deposits at 2 and 3 m distance from the field edge (Fig. 2, Tab. A1, appendix). At 2 and 3 m from the field edge 17 % and 50 %, respectively, of measurements were below detection level.

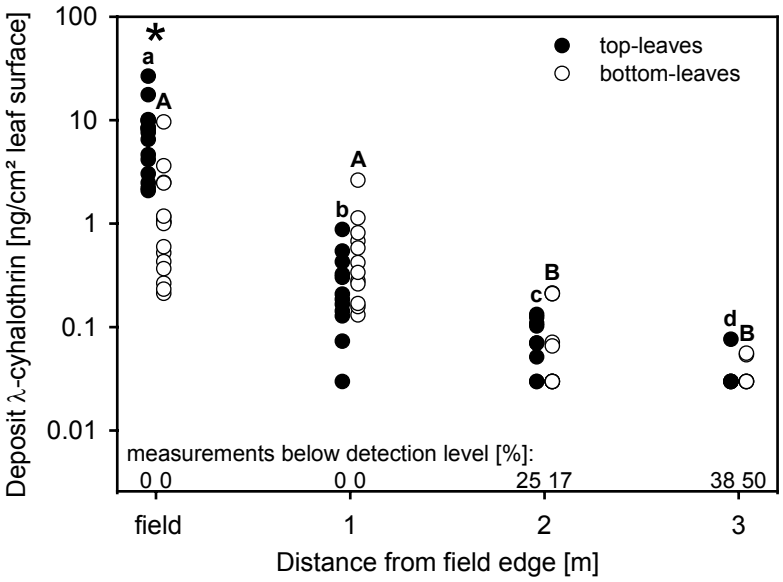

Fig. 2. Lambda-cyhalothrin leaf deposits on broad beans exposed to insecticide spray within wheat fields and to spray drift within field margin strips at 1, 2, and 3 m distance from the field edge of fields 1 & 2 in 2002. Different lowercase (uppercase) letters indicate significant differences between top-leaf (bottom-leaf) deposits at $p < 0.0083$. Asterisks indicate significant difference between deposits on top- and bottom-leaves at the same distance from the field edge.
Results Wilcoxon rank test (field): $N = 16$, $z = -3.52$, $p < 0.001$. Results ATS: (top): $df = 48$, $F = 79.40$, $p < 0.001$; (bottom): $df = 48$, $F = 47.23$ $p < 0.001$.

During insecticide application to field 3 in 2002, the wind blew moderately at an angle of 60° to the field margin strips. These nearly perfect conditions resulted in higher drift deposits at 1, 2, and 3 m distance from the field edge compared to the application to fields 1 and 2 (Tab. 2). Overall, just 8 % of measurements (top-leaf, 3 m) were below detection level (Fig. 3). Deposits on top-leaves decreased significantly with distance from the field edge, however, deposits at 2 and 3 m did not differ from each other (Fig. 3). Deposits on bottom-leaves within-crop did not differ significantly from deposits at 1 m, but both were higher than deposits at 2 and 3 m distance from the field edge

(Tab. A1, appendix). Due to a short rainfall while leaf samples from within-crop were collected, which resulted in a visible dissolving of the insecticide-tracer deposits on leaf surfaces, deposits on leaves from within-crop were lower compared to deposits from the same sample positions in the other trials (Tab. 2). At that time leaf samples at 1, 2, and 3 m distance from the field edge had already been sampled, i.e. drift deposits had not been affected by rain.

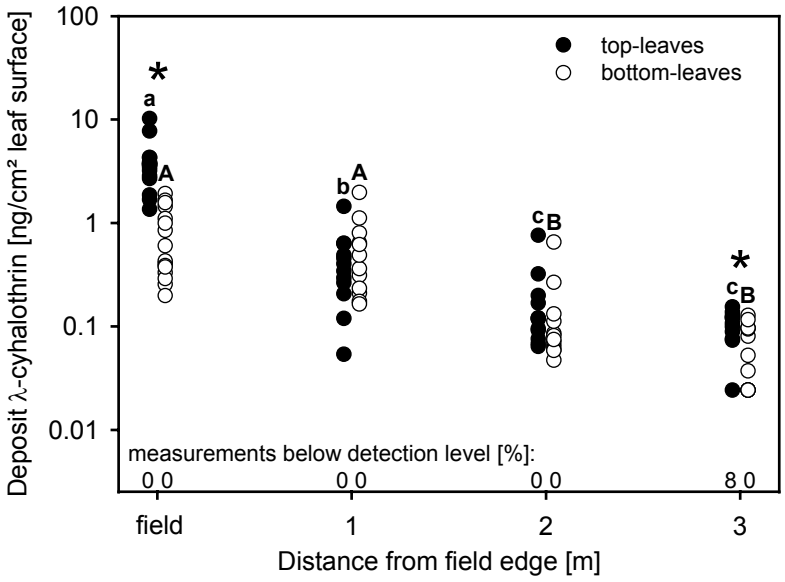

Fig. 3. Lambda-cyhalothrin leaf deposits on broad beans exposed to insecticide spray within wheat fields and to spray drift within field margin strips at 1, 2, and 3 m distance from the field edge of field 3 in 2002. Different lowercase (uppercase) letters indicate significant differences between top-leaf (bottom-leaf) deposits at $p < 0.0083$. Asterisks indicate significant difference between deposits on top- and bottom-leaves at the same distance from the field edge.
Results Wilcoxon rank test: (field): $N = 16$, $z = -3.46$, $p < 0.001$; (3m): $N = 16$, $z = -2.04$; $p = 0.041$. Results ATS: (top): $df = 48$, $F = 42.77$, $p < 0.001$; (bottom): $df = 48$, $F = 31.46$ $p < 0.001$.

During insecticide application to fields 1 and 2 in 2003, the wind blew moderately to strong at an angle of 53° to the weed strips (Tab. 1). Mean values of drift deposits on top- as well as on bottom-leaves were higher compared to the other trials (Tab. 2). Deposits on top-leaves at 1 m did not differ from deposits at 2 m from the field edge but were significantly higher than deposits at 3 m. Deposits at 2 and 3 m distance did not differ from each other (Fig. 4, Tab. A1, appendix). Deposits on bottom-leaves within-crop did not differ significantly from deposits on bottom-leaves at 1 m, but both were significantly higher compared to deposits at 2 and 3 m distance from the field edge. Deposits on bottom-leaves at 2 and 3 m did not differ from each other (Tab. A1, appendix). Pairwise comparison revealed significantly higher deposits on top-leaves at

3 m from the field edge compared to bottom-leaves. Overall, just 8 % of measurements were below detection level (Fig. 4).

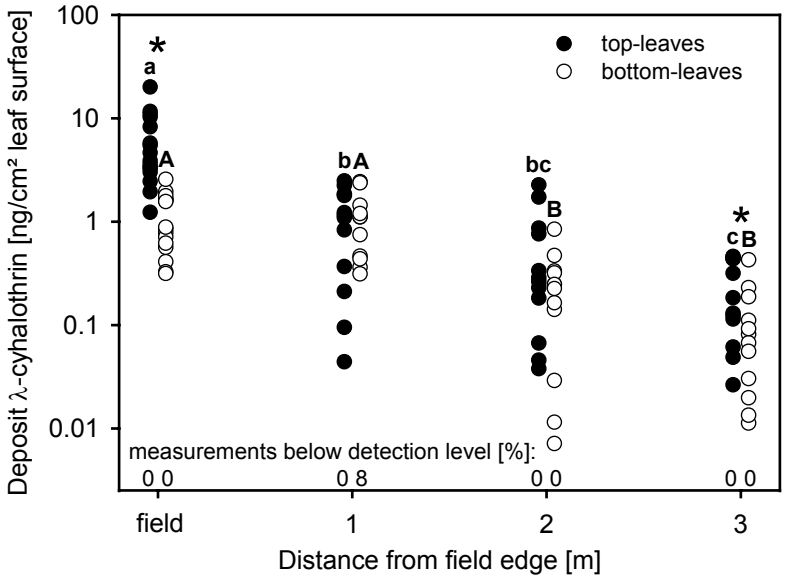

Fig. 4. Lambda-cyhalothrin leaf deposits on broad beans exposed to insecticide spray within wheat fields and to spray drift within field margin strips at 1, 2, and 3 m distance from the field edge of fields 1 & 2 in 2003. Different lowercase (uppercase) letters indicate significant differences between top-leaf (bottom-leaf) deposits at $p < 0.0083$. Asterisks indicate significant difference between deposits on top- and bottom-leaves at the same distance from the field edge.
Results Wilcoxon rank test: (field): $N = 16$, $z = -3.36$, $p < 0.001$; (3 m): $N = 16$, $z = -2.82$, $p = 0.002$. Results ATS: (top): $df = 48$, $F = 28.06$, $p < 0.001$; (bottom): $df = 48$, $F = 25.93$ $p < 0.001$.

During insecticide application to field 3 in 2003, the wind did not blow towards but nearly parallel to weed strips (Tab. 1), resulting in low drift deposition into the field margin. This is reflected by the high proportions of measurements below detection level (Fig. 5). Within-crop deposits on bottom-leaves were significantly higher compared to drift deposits at 1 m from the field edge, and furthermore, these on both top- and bottom-leaves at 1 m distance from the field edge were significantly higher compared to deposits at 3 m (Fig. 5, Tab. A1, appendix). Deposits on both top- and bottom-leaves at all other distances from the field edge did not show any significant difference (Fig. 5).

In both years, deposit measurement proved the non-contamination of covered control field margins.

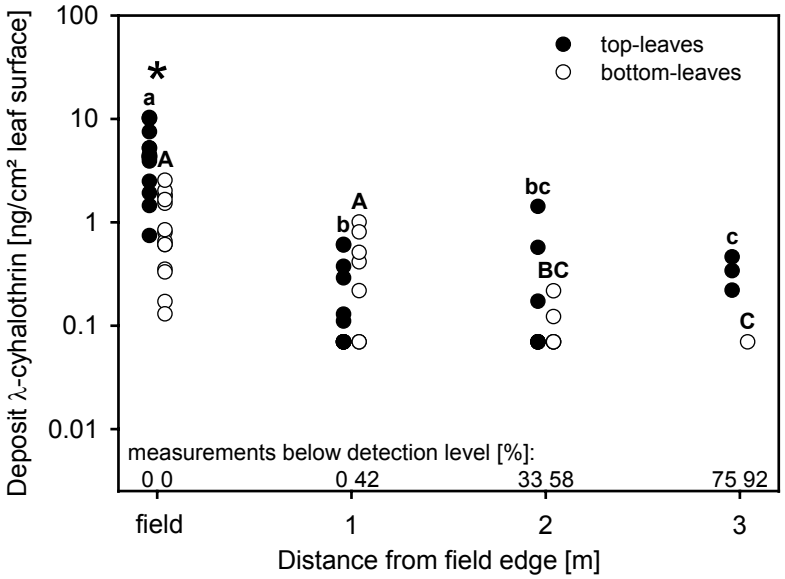

Fig. 5. Lambda-cyhalothrin leaf deposits on broad beans exposed to insecticide spray within wheat fields and to spray drift within field margin strips at 1, 2, and 3 m distance from the field edge of field 3 in 2003. Different lowercase (uppercase) letters indicate significant differences between top-leaf (bottom-leaf) deposits at $p < 0.0083$. Asterisks indicate significant difference between deposits on top- and bottom-leaves at the same distance from the field edge.
Results Wilcoxon rank test (field): $N = 16$, $z = -3.41$, $p < 0.001$. Results ATS: (top): $df = 48$, $F = 37.16$, $p < 0.001$; (bottom): $df = 48$, $F = 25.93$ $p < 0.001$.

Tab. 2. Mean deposits of λ-cyhalothrin [ng/cm²] ± SE on leaf surfaces of broad beans exposed to insecticide spray within wheat fields and to insecticide spray drift within field margin strips at 1, 2, and 3 m distance from the field edge.

	Mean deposits λ-cyhalothrin [ng/cm²] leaf surface ± SE							
	top-leaves				bottom-leaves			
	field	1 m	2 m	3 m	field	1 m	2 m	3 m
2002								
field 1&2	8.24 ± 1.59	0.28 ± 0.07	0.06 ± 0.01	0.02 ± 0.01	1.64 ± 0.58	0.63 ± 0.20	0.08 ± 0.02	0.02 ± 0.01
field 3	3.89 ± 0.55	0.45 ± 0.11	0.18 ± 0.06	0.09 ± 0.01	0.80 ± 0.14	0.59 ± 0.15	0.14 ± 0.05	0.07 ± 0.01
2003								
field 1&2	6.24 ± 1.64	1.12 ± 0.32	0.59 ± 0.28	0.23 ± 0.07	1.14 ± 0.23	1.00 ± 0.30	0.25 ± 0.09	0.11 ± 0.05
field 3	5.04 ± 1.01	0.21 ± 0.08	0.21 ± 0.16	0.09 ± 0.06	1.06 ± 0.26	0.26 ± 0.14	0.05 ± 0.03	0.01 ± 0.01

2.3.3 Toxicity of deposits on plant surfaces to A. colemani

Figures 6 to 11 show control-adjusted mortalities of *A. colemani* subjected for 12 and 24 hours, respectively, to drift deposits of λ-cyhalothrin on broad bean leaves exposed at different distances from the field edge.

Deposits originating from insecticide application to fields 1 and 2 in 2002 caused mean corrected mortalities of ≤ 30 % to *A. colemani* within the first 12 hours of exposure. Neither were there significant differences between mortality levels at different distances from the field edge (Tab. A2, appendix) nor between mortalities on top-leaves and mortalities on bottom-leaves at a given distance (Fig. 6). Twenty-four hours post-exposure, an increase in mortalities of *A. colemani* was observed on plants from each distance from the field edge (Fig. 7). Mean mortalities ranged from 35 % (top-leaf, within-crop) to 17 % (top-leaf, 3 m) (Fig. 7). On top-leaves mortalities of *A. colemani* slightly decreased with distance from the field edge, but mortalities did not differ statistically (Tab. A2, appendix). On bottom-leaves mean mortalities at 1 m (23 %), 2 m (23 %), and 3 m (22 %) were similar; within-crop mortality (30 %) was just marginally and insignificantly higher (Fig. 7). Pairwise comparisons showed no significant differences between mortalities on top- and bottom-leaves on plants from the same distance after 24 hours of exposure (Fig. 7). Twelve and 24 hours post-exposure, respectively, mortalities on plants from the same distance were highly variable, both on top- and bottom-leaves.

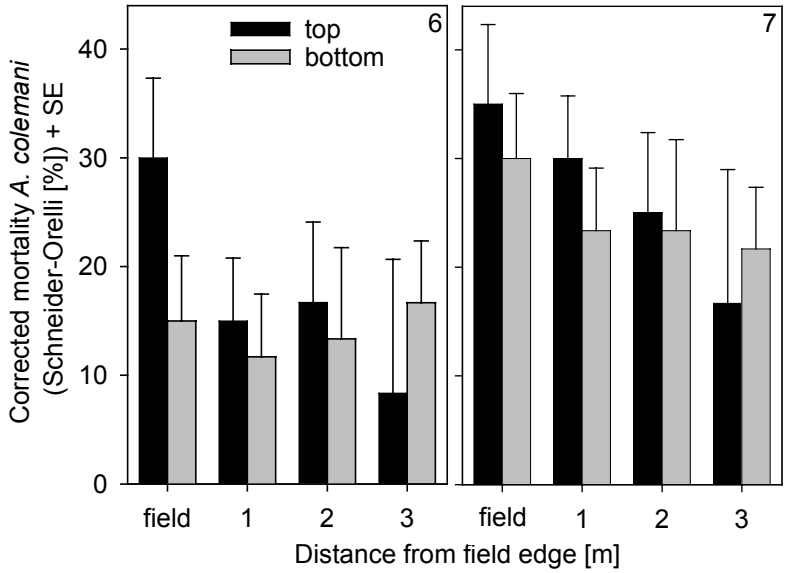

Fig. 6 & 7. Mean corrected mortalities [%] + SE of adult *A. colemani* exposed for 12 (Fig. 6) and 24 hours (Fig. 7) to λ-cyhalothrin deposits on top- and bottom-leaves of broad beans exposed to spray (drift) at different distances from the field edge of fields 1 & 2 in 2002.

Due to the rainfall interference with drift deposition on bean plants prior to field removal, toxicity data of *A. colemani* exposure to deposits produced by the application to field 3 in 2002 are not presented. There was obviously no correlation between observed corrected mortalities (range from -1.7 % to 7.2 % after 24 hours of exposure) and measured spray drift deposits.

Deposits originating from insecticide application to fields 1 & 2 in 2003 caused control-adjusted mortalities < 20 % on top-leaves within 12 hours of exposure (Fig. 8). Mean mortality levels recorded on plants from 1 m (15.9 %) and 2 m (19.7 %) were higher, though insignificantly, than mortality on within-crop top-leaves (11.7 %). Mortality levels on bottom-leaves were very low, ranging from 1.0 % to 10.3 %. Neither were there significant differences between mortality levels at different distances from the field edge (Tab. A2, appendix) nor between mortalities on top-leaves and mortalities on bottom-leaves at a given distance (Fig. 8). Within the ensuing 12 hours, mortalities increased on plants from all distances on top- as well as on bottom-leaves (Fig. 9). On top-leaves, mortality was highest within-crop (42.9 %) but did not differ significantly from mortalities on drift collector plants (27.6 % to 31.4 %). On bottom-leaves mortality was lowest, although not significant, within-crop (19.3%), whereas a trend of higher mortalities was recorded at 1, 2, and 3 m (27.0 %). Mortality rates on plants from within-crop were significantly higher on top-leaves than on bottom-leaves (Wilcoxon rank test: df = 16, z = -2.24, p = 0.023).

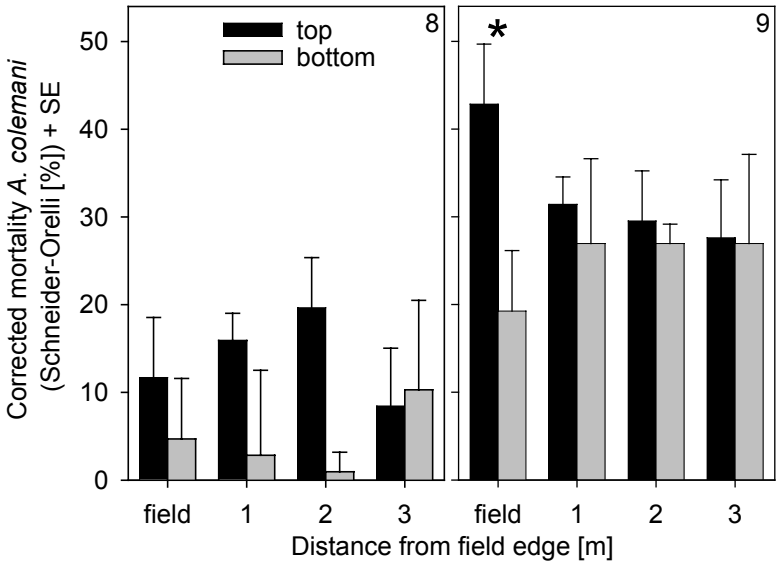

Fig. 8 & 9. Mean corrected mortalities [%] + SE of adult *A. colemani* exposed for 12 (Fig. 8) and 24 hours (Fig. 9) to λ-cyhalothrin deposits on top- and bottom-leaves of broad beans exposed to spray (drift) at different distances from the field edge of fields 1 & 2 in 2003. Asterisks indicate significant difference between mortality on top- and bottom-leaves.

Twelve hours post-exposure mean mortalities caused by deposits originating from insecticide application to field 3 in 2003 ranged from 30.3 % (within-crop) to 14.3 % (2 m) on top-leaves and from 20.7 % (1 m) to 6.3 % (2 m) on bottom-leaves. Mortality levels of *A. colemani* on plants from different distances did not differ significantly from each other (Tab. A2, appendix). Pairwise comparisons revealed significantly higher mortality on within-crop top-leaves (30.3 %) compared to mortality on bottom-leaves (8.1 %) (Wilcoxon rank test: df = 16, z = -2.11, p = 0.039) (Fig. 10). Mortality rates increased with increasing exposure time on plants from all distances from the field edge (Fig. 11). On top-leaves, mortality on plants from within-crop (56 %) was significantly higher than mortality on plants from 2 m distance from the field edge (25 %) but it did not differ significantly from mortalities at 1 m (45 %) and 3 m (26 %). Corrected mortalities of parasitoids on top-leaves of drift collector plants from 1, 2, and 3 m were similar (Tab. A2, appendix). On bottom-leaves, mean control-corrected mortality within-crop (41 %) was significantly higher than mortality on plants from 3 m distance (15 %) but it did not differ from mortalities on plants from 1 m (41 %) and 2 m (17 %) (Fig. 11, Tab. A2, appendix). There were no significant differences among mortalities on bottom-leaves on plants from 1, 2, and 3 m. In addition, pairwise comparisons showed that 24 hours post-exposure mortalities on top- and bottom-leaves on plants from the same distance did not differ significantly from each other (Fig. 11).

After 24 hours, the mean mortality of *A. colemani* in the control treatment was 0.9 % in 2002 and 12.1 % in 2003, thus the recommended threshold value of 13 % (Mead-Briggs et al., 2000) was respected.

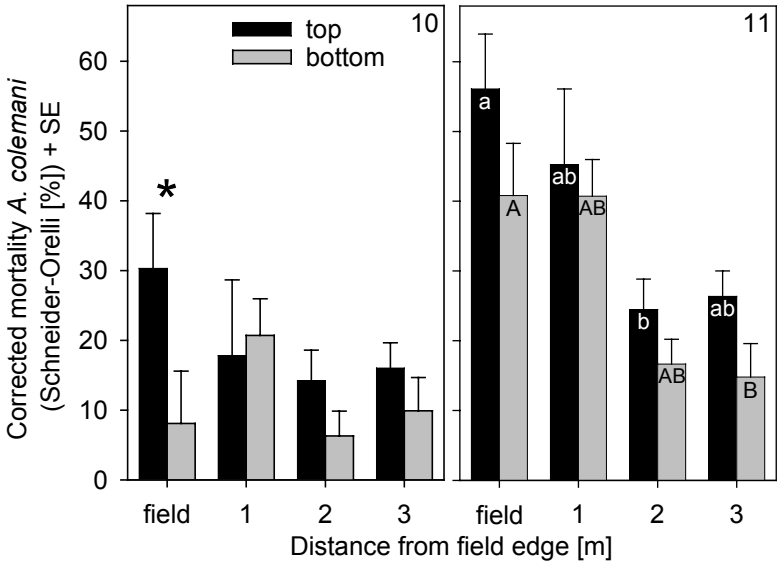

Fig. 10 & 11. Mean corrected mortalities [%] + SE of adult *A. colemani* exposed for 12 (Fig. 10) and 24 hours (Fig. 11) to λ-cyhalothrin deposits on top- and bottom-leaves of broad beans exposed to spray (drift) at different distances from the field edge of field 3 in 2003.
Asterisks indicate significant difference between mortality on top- and bottom-leaves.
Different lowercase (uppercase) letters indicate significant differences between mortalities on top-leaves (bottom-leaves) at $p < 0.0083$.
Results ATS: (top): df = 16, F = 3.44, p = 0.043; (bottom): df = 16, F = 5.14, p = 0.012.

2.3.4 Toxicity of deposits on plant surfaces to C. septempunctata

Figures 12 and 13 illustrate the corrected mortalities of *C. septempunctata* larvae exposed for three, 12, and 24 hours to drift deposits of λ-cyhalothrin on top-leaves of bean plants from different distances from the field edge.

Deposits originating from insecticide application to fields 1 6 2 (2003) caused high mortalities of *C. septempunctata* larvae within three hours of exposure on plants from within-crop (77.1 %) (Fig. 12). Mean control-adjusted mortality within-crop did not differ significantly from mortalities on drift collector plants from 1 m (58.3 %) but was significantly higher than mortality on plants from 2 m (36.1 %) and from 3 m (11.1 %). In addition, a significant difference was identified between mortalities on plants from 1 m and 3 m, whereas all other combinations did not differ significantly from each other (Tab. A3, appendix). Mortality checks 12 hours post-exposure of *C. septempunctata* larvae to deposits revealed an increase in mortalities to more than 50 % on plants from all distances (Fig. 12). No significant differences among mortality levels were found. Within the ensuing 12 hours of exposure mortalities on plants from within-crop and from 1 m from the field edge increased. Mortality rates of larvae on plants from within-

crop (92 %) did not differ significantly from mortalities on drift collector plants from 1 m (73 %) and 2 m (66 %), but were significantly higher than mortalities on plants from 3 m (46 %) (Tab. A3, appendix). Twenty-four hours post-exposure, mortalities of ladybeetle larvae exposed to drift deposits on plants from 1, 2, and 3 m from the field edge did not differ significantly from each other (Fig. 12).

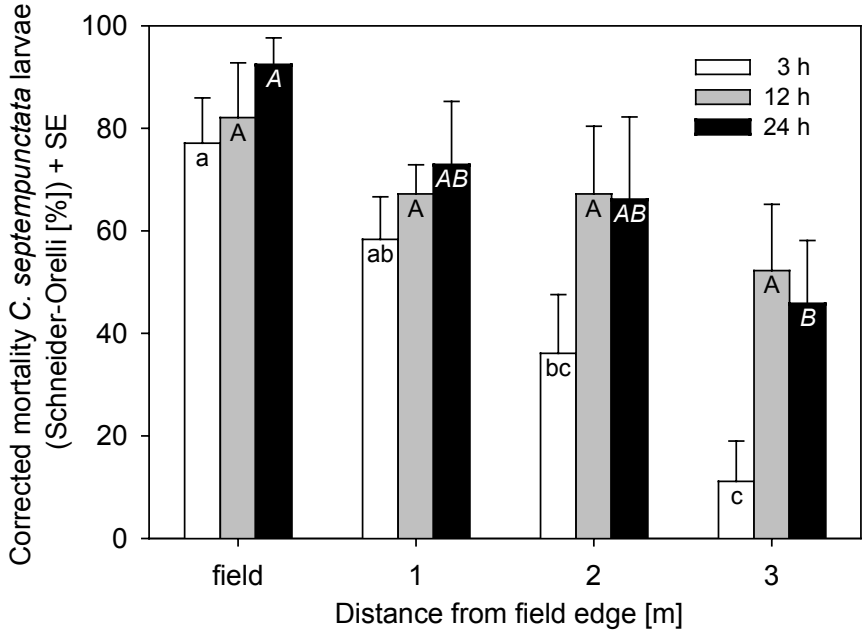

Fig. 12. Mean corrected mortalities (Schneider-Orelli) [%] + SE of *C. septempunctata* larvae exposed for 3, 12, and 24 hours to λ-cyhalothrin deposits on top-leaves of broad beans exposed to insecticide spray within wheat fields and to insecticide drift within field margin strips at distances of 1, 2, and 3 m from the field edge of field 1 & 2. Different lowercase, uppercase and italic uppercase letters indicate significant differences between mortalities assessed after 3, 12, and 24 hours of exposure, respectively, at $p < 0.0083$.
Results ATS: (3 h): df = 16, F = 9.91, $p < 0.001$; (24 h): df =16, F = 3.33, p = 0.048.

Exposure of *C. septempunctata* larvae to deposits originating from insecticide application to field 3 (2003) caused mean corrected mortalities of 62.5 % and 69.4 % on plants from within-crop and from 1 m, respectively; both mortality levels were significantly higher than those on plants from 2 and 3 m (8.3 % each) (Fig. 13, Tab. A3, appendix). Further exposure of larvae to deposits resulted in increasing mortalities on plants from within-crop to 95.7 %, on plants from 1 m to 79.7 %, and on plants from 2 m to 18.8 %, whereas a decrease in corrected mortalities to 4.3 % was recorded on plants from 3 m (Fig. 13). No significant differences were identified between mortalities on plants from within-crop and from 1 m as well as between mortalities on plants from 2 m and 3 m from the field edge. Mortality rates recorded 24 hours post-exposure did

not differ greatly from mortalities observed after 12 hours of exposure (Fig. 13). High mortality levels were recorded on plants from within-crop (97.8 %) as well as on plants from 1 m distance (79.7 %). Both mortality values were significantly higher compared to mortalities on plants from 2 m (21.7 %) and 3 m (4.3 %) from the field edge (Tab. A3, appendix).

After 24 hours, mortality of *C. septempunctata* in the control treatments did not exceed the recommended threshold value of 30 % (Schmuck et al., 2000).

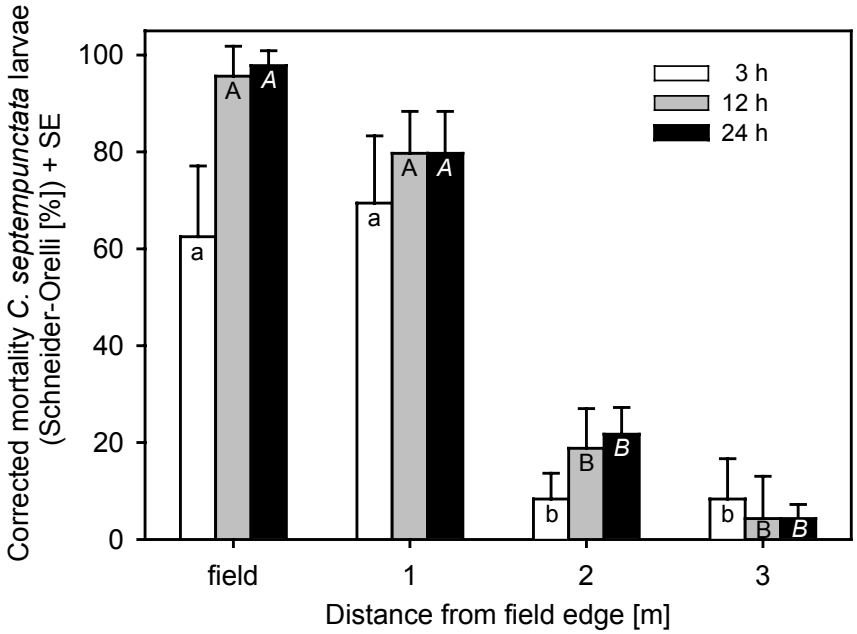

Fig. 13. Mean corrected mortalities (Schneider-Orelli) [%] + SE of *C. septempunctata* larvae exposed for 3, 12, and 24 hours to λ-cyhalothrin deposits on top-leaves of broad beans exposed to insecticide spray within wheat fields and to insecticide drift within field margin strips at distances of 1, 2, and 3 m from the field edge of field 3. Different lowercase, uppercase and italic uppercase letters indicate significant differences between mortalities assessed after 3, 12, and 24 hours of exposure, respectively, at $p < 0.0083$.
Results ATS: (3 h): df = 16, F = 11.56, $p < 0.001$; (12h): df = 16, F = 24.98, $p < 0.001$; (24 h): df =16, F = 32.82, $p < 0.001$.

2.3.5 Relationship between insecticide deposits and mortality of A. colemani *and* C. septempunctata

Nonparametric correlation proved the positive relationship between deposits of λ-cyhalothrin on leaf surfaces and mortalities of *A. colemani* exposed for 12 hours ($N = 456$, $r_s = 0.312$, $p < 0.001$) as well as for 24 hours ($N = 456$, $r_s = 0.510$, $p < 0.001$) to deposits on a closely adjoining leaf. The value of Spearman's rank correlation coefficient, r_s, indicates that the relationship between deposits and mortality of *A. colemani* was stronger after 24 hours than after 12 hours of exposure.
The relationships between deposits of λ-cyhalothrin and mortality of *C. septempunctata* larvae exposed for three hours ($N = 152$, $r_s = 0.739$, $p < 0.001$), 12 hours ($N = 152$, $r_s = 0.776$, $p < 0.001$), and 24 hours ($N = 152$, $r_s = 0.779$, $p < 0.001$) to deposits did not differ greatly from each other. The value of r_s indicates a stronger relationship between deposits and mortality of *C. septempunctata* larvae compared to the relationship between deposits and mortality of *A. colemani*.

2.4 DISCUSSION

2.4.1 Drift deposition

During insecticide applications wind speed and wind direction towards the weed strips did not perfectly meet the desired conditions, i.e. wind > 2 m/s that blew at an angle of 90° (± 30°) to the field margin strips (Ganzelmeier et al., 1992; anonymous, 2003b). The extensive preparatory work (e.g. rearing of test plants and insects) narrowed the opportunities to execute the experiment under optimal meteorological conditions.
Measurement of spray drift deposition demonstrated the influence of wind speed and direction on drift deposition into the sown weed strips. Deposits on both top- and bottom-leaves were higher when the wind speed was moderate during the insecticide application (field 3, 2002 and fields 1 & 2, 2003) compared to the applications during which it was slow (fields 1 & 2, 2002) or nearly parallel towards the field margin strips (field 3, 2003). In addition to wind speed, spray droplet size is one of the most important factors affecting the downwind distance that a droplet will move (Kaul et al., 2001a,b; Koch et al., 2004b). The velocity at which a droplet falls to the ground depends on the size of the droplet, i.e. small lightweight droplets remain airborne for a longer time and are therefore more susceptible to drift than larger, heavier droplets.

Therefore, depending on the droplet size spectrum, even low wind will transport spray droplets to off-crop areas. In the current study approximately 10-15 % of drift-prone droplets (< 100 µm) were produced using the standard nozzle type at the adjusted operating pressures. Thus, even at very slow wind speeds of 0 to 1 m/s (fields 1 & 2, 2002) deposits were measured up to 3 m from the field edge.

Within-crop, insecticide deposits on top-leaves were always significantly higher compared to the one on bottom-leaves. The difference between within-crop top and bottom deposits was due to the dense plant cover of the wheat that resulted in a strong filtering effect of the wheat plants. At growth stage BBCH 61 to 69 the interception of a winter wheat crop canopy ranges between 76 % and 98 % (Becker et al., 1999) resulting in reduced soil deposits. A body of literature has expounded large reduction in soil deposits on the top of the canopy due to wheat density (e.g. Gyldenkærne et al., 1999; Kühne et al. 2002; Jensen & Spliid, 2003). In the current study, off-crop drift deposits on top-leaves were not significantly higher than drift deposits on bottom-leaves, except for two samples at 3 m distance from the field edge. This result was unexpected, contrasting with higher deposits on top-leaves compared to bottom ones. Kühne et al. (2002) found considerable differences in drift deposits on artificial collectors (pipe cleaners) arranged at the bottom and the top of a grass- and weed-dominated field margin canopy. Scientists explained these differences by the filtering effect of the vegetation in vertical direction. In the current study, compared to the homogenous density of the wheat stand, the weed strip canopy was structurally diverse with a patchy density, which may have resulted in a heterogeneous filtering capacity. However, the most striking reason for the unverifiable difference between top and bottom deposits may be attributed to the high variability of deposits (see below). At all distances, 95th percentiles of drift deposits on bottom-leaves calculated in the current study are lower compared to 95th percentile drift data of the German spray drift model (Ganzelmeier et al., 1995) used in exposure assessments for terrestrial non-target arthropods (Candolfi et al., 2001). For this spray drift model, soil deposits were assessed by measuring drift deposits on artificial collectors (slides) deployed on bare ground at different distances from the sprayed crop. Lower deposits in the current study clearly demonstrate the existing filtering effect of the field margin canopy. Since the magnitude of the drift is influenced by technical and meteorological conditions, results from the current study cannot be directly compared to drift deposit measurements performed under different climatic and technical conditions.

In the present work, the mean deposits on bottom-leaves at 1 m from the field edge were higher than deposits on top-leaves at 1 m, whereas mean deposits on bottom-leaves at 2 and 3 m from the field edge were lower compared to respective top-leaf deposits. These high deposits on bottom-leaves at 1 m may be the result of application-inherent irregularities. Driving over bumpy ground causes tractor boom movements (pitch and yaw) during application, which often results in drift peaks at short distances from the field edge (Longley et al., 1997b; Koch et al., 2003). Due to fan geometry boom movements can even result in overspray of field margins (Koch et al., 2003). These factors may offer a potential explanation of the high deposits on bottom-leaves at 1 m from the field edge.

Drift deposition on leaf surfaces of bean plants exposed within field margin strips was characterised by its patchiness, i.e. deposits on equidistant leaves of the sprayed crop were highly variable. This patchiness is associated with the interception process within a plant canopy. In contrast to the retention of insecticide spray on in-crop plants during an insecticide application, which is characterised by droplet shatter, bounce, or runoff, drifting particles are retained at any hit solid surface (Koch et al., 2004b). In addition, interception of drifting particles on off-crop plant surfaces is not influenced by structural differences of plant surfaces or the phyllotaxy (Koch & Weißer, 2004). Within a closed vegetation airflows carrying drift particles travel along meandering trajectories due to turbulences and lose drift particles by deposition on moving plant elements (Raupach et al., 2000), resulting in heterogeneous point-like deposits (Koch et al., 2003, 2004a,b). Sudden changes of wind speed or direction and the structural diversity of plant covers make the interception of pesticide drift in natural vegetation a very complex and random process. Therefore, in a bulk of studies, variability in spray drift data was lessened by measuring drift over an area of no or short vegetation (e.g. Sinha et al., 1990; Davis et al., 1991a,b, Ganzelmeier et al., 1995; van de Zande, 2001). Thereby turbulences or deflection of wind are curtailed (Davis et al., 1991b; Davis et al., 1994) and the filtering effect of vegetation is not incorporated into these studies. In addition, variability is often confined through the usage of artificial spray drift collectors. Various artificial collectors have been used so far, e.g. water sensitive papers, pipe cleaners, petri dishes, plastic hair curlers, or synthetic cleaning pads. The advantage of such artificial collectors resides in their uniformity in size and shape. Furthermore, they can more easily be arranged at defined inclinations and positions within a field margin. On the other hand, artificial collectors suffer from limitations since they lack the ability to fully represent the complex morphology of natural collectors (e.g. plants). In the current study, broad beans were exploited as natural drift collectors. Their leaves were

hardly ever uniform in size, shape, and inclination, thereby possessing the structural and spatial variability of natural collectors. The aim of drift deposit measurements should be a realistic mapping of drift deposits on natural surfaces since they reflect possible exposure scenarios for non-target organisms. The approach of reducing variability in spray drift data by measuring drift over an area of no or short vegetation and/or by using artificial collectors is misleading since one of the most important characteristics of drift, patchiness, is ignored. In a series of drift studies using the contact herbicide Gramoxone® extra (paraquat) that causes contact burn on plant foliage, Koch et al. (2004a) visualised the variability of drift deposition on plant surfaces. Their results impressively showed the patchy pattern of paraquat symptoms due to drift deposition, both, in horizontal and vertical direction in plant canopies. High variability in drift depositions found in the current study and other studies, where drift into off-crop plant canopies was measured (Kühne et al., 2002; Koch et al., 2004a,b) indicate that deposits on plants at defined distances from the field edge and the associated risks for non-target organisms are hard to predict.

For the registration of plant protection products in the European Union, the hazards of pesticides to non-target arthropods should not only be assessed for in-field exposure but also for off-field exposure (Candolfi et al., 2001). In the current risk assessment procedures, the potential off-field hazards for non-target arthropods are derived from application rates, LR_{50} values from laboratory testing, and the 90^{th} percentile drift values for a distance of 1 m from the field edge based on the German spray drift model (Ganzelmeier et al. 1995; BBA, 2000; Candolfi et al., 2001). Since these drift values were determined under “worst case” conditions (see above) it was decided to correct these overestimated values by a “vegetation distribution factor” (Candolfi et al., 2001). This means a corrected 90^{th} percentile of 0.277 % is used for the calculation of off-crop hazards. The corresponding 90^{th} percentiles on bottom-leaves within field margin strips at 1 m distance from the field edge calculated in the current study are much higher and range from 3.22 % to 1.26 %. Using standard and 50 % drift reducing nozzles, Koch et al. (2003) also found higher drift deposits in plant canopies at 1 m distance from the field edge compared to the basic drift values of the BBA (Ganzelmeier et al., 1995). However, for farther distances the latter study found lower deposits. These results indicate that auxiliary studies on drift deposition into off-crop plant canopies are obviously needed for a reliable exposure assessment for terrestrial non-target arthropods. In addition, if vegetation distribution factors are used for the correction of the BBA drift data, these factors should be specific to different-structured plant

canopies, which can differ in their retention areas and filter capacities due to differences in vegetational architecture (Koch & Weißer, 2004).

2.4.2 Exposure bioassay A. colemani

Within 12 hours past exposure to deposits, mortality rates of *A. colemani* remained relatively low and did not exceed 30 % on plants from within-crop and 20 % on plants from off-crop, respectively. The prolongation of the exposure time to 24 hours caused an increase in mortalities. Increasing mortality of *Aphidius* species with increasing exposure time to various insecticide deposits have been shown in several studies (e.g. Krespi et al., 1991; Maise et al., 1996; Longley & Jepson, 1997a). In both study years mortalities > 50 % of *A. colemani* within 24 hours after exposure were just recorded in few replicates on both top- and bottom-leaves within-crop as well as at 1 m distance from the field edge. In addition, mortality > 50 % was observed in a single replicate in 2002 on top-leaves at 3 m distance. Mortality levels of *A. colemani* caused by deposits on bean leaf surfaces at all other positions within weed strips were < 50 %. Mortalities of the parasitoids observed in the current study are approximately in line with findings of Kühne et al. (2002). By connecting λ-cyhalothrin spray drift deposit pattern with mortality data from laboratory testing, they predicted mortality levels of more than 50 % for *A. rhopalosiphi* at a distance of 1 m from the field edge both at the bottom and the top of the canopy. At farther distances, the risks for this parasitoid species were found to be lower, although drift deposit pattern showed that peak deposits may cause > 50 % mortality up to a distance of 5 m from the sprayed field.

The application of the recommended field rate of λ-cyhalothrin to wheat fields produced mean spray deposits on within-crop top-leaves of 8.24 (fields 1 & 2, 2002), 6.24 (fields 1 & 2, 2003) and 5.04 ng a.i./cm² leaf surface (field 3, 2003). These deposits caused mean corrected mortalities of 35 %, 43 % and 56 % respectively of *A. colemani* exposed for 24 hours to deposits. Although data shortage prohibited the calculation of LR_{50} values, referring to the literature illustrated that mortality levels noted in the current study are in accordance with these published for two other *Aphidius* species. After an exposure to treated glass surfaces for 24 hours the estimated LR_{50} value was 4.97 ng λ-cyhalothrin/cm² for *Aphidius ervi* Haliday (Desneux et al., 2004) and 5.9 ng λ-cyhalothrin/cm² for *A. rhopalosiphi* (Kühne et al., 2002). However, comparisons should be done with care since toxicity factors can vary with different exposure conditions. Additionally, bioavailability of insecticide deposits on different surfaces may vary and

thus produce different mortalities in test organisms (Longley & Jepson, 1997a). Species-specific differences in sensitivity to insecticides within the order *Aphidius* are also possible. Maise et al. (1996) compared the sensitivity of *A. colemani*, *A. rhopalosiphi* and *Aphidius matricariae* Haliday to the insecticide dimethoate on glass plates and found comparable dose-response relationships for *A. colemani* and *A. rhopalosiphi* but a weaker dose-response for *A. matricariae*. To our knowledge no other studies have been conducted so far that compared the sensitivity of different *Aphidius* species to plant protection products.

In 2003 the reduced application rate of Trafo® resulted in lower initial spray deposits of λ-cyhalothrin on within-crop leaf surfaces compared to 2002. Surprisingly, mean levels of within-crop mortality of *A. colemani* in 2003 were higher compared to mortalities in 2002. This finding suggested that *A. colemani* were more susceptible to deposits of λ-cyhalothrin in 2003 than in 2002, which may be explained by differences in fitness parameters of parasitoids. Differences in control mortalities between both years (2002: 0.9 %; 2003: 12.1 %) may indicate differing vigour of test organisms. Fernández & Nentwig (1998) assessed quality parameters, i.e. adult mortality, longevity, flight capacity, and parasitation rate, of *A. colemani* delivered by different Central European suppliers of biocontrol agents. They concluded that the quality of *A. colemani* is often unsatisfactory and that quality of products delivered by the same producer often differs. Conditions during the transport influenced the quality greatly. In relation to the current study, quality differences in *A. colemani* between both years probably caused differences in their susceptibility towards λ-cyhalothrin and thus in mortalities.

Overall, mortality levels of *A. colemani* exposed to deposits on either top- or bottom-leaves did not significantly differ among plants from different distances from the field edge. This finding agrees with the patchiness of drift deposits on leaf surfaces. The highly erratic spray drift deposits resulted in highly variable exposure scenarios on plants from the same distance from the field edge. As pointed out above, drift deposition at a certain distance is hardly predictable. Drift deposit measurement carried out in the current study indicated that non-controllable factors (e.g. sudden changes in wind speed or direction, boom movements due to bumpy ground) can produce peak deposits causing high mortalities. On the other hand, a sudden slow-down of the wind speed or the shading of the surrounding vegetation can result in low deposits and low mortalities, even at short distances from the field edge. Mappings of spray drift deposition pattern within a field margin support this finding (Kühne et al., 2002).

2.4.3 Exposure bioassay C. septempunctata

Deposits of λ-cyhalothrin exhibited greater toxicity to *C. septempunctata* larvae compared to adult *A. colemani*. Ladybeetle larvae showed a rapid reaction to deposits resulting in high mortalities within three hours after exposure. This was possibly caused by a higher insecticide uptake relative to *A. colemani* due to contact not only with tarsi but with further body parts to the leaf, e.g. with thorax and abdomen during resting periods. Heneghan et al. (1995) quantified the uptake of the insecticide diazinon by *A.* ervi and adult *Hippodamia convergens* Guérin-Méneville after 24 hour exposure on treated leaf surfaces. They found up to 200fold more diazinon in *H. convergens* than in *A. ervi.*

Increasing the duration of exposure from three to 12 hours caused an increase in mortality levels of *C. septempunctata* larvae up to an asymptote at 24 hours. Literature records have shown high susceptibility of coccinellid species towards λ-cyhalothrin. The topical application of λ-cyhalothrin to adult *Pullus mediterraneus* Fabricius resulted in high and rapid mortality in the test organisms (Ba M´hamed & Chemseddine, 2002). Sterk et al. (1999) found nearly 100 % mortality in larvae and adults of *Semiadalia undecimnotata* (Schneider) after exposure to deposits of λ-cyhalothrin on glass plates. In addition, several field studies have shown effects of λ-cyhalothrin spray on Coccinellidae at population level. Significantly reduced densities of coccinellid larvae were found following applications of various doses (between 2.5 and 10 g a.i./ha) of λ-cyhalothrin in wheat (Niehoff, 1996; Wick & Freier, 2000). The application of 26.2 and 13.1 g λ-cyhalothrin/ha, respectively, to sweet corn significantly reduced population densities of the ladybeetles *Coleomegilla maculata* De Geer and *Harmonia axyridis* (Pallas) (Musser & Shelton, 2003). The application of λ-cyhalothrin at a rate of 12.8 g a.i./ha to cotton caused 93 % mortality to adult *C. maculata* when exposed for 48 hours to leaf deposits (Tillmann & Mulrooney, 2000). Under the same bioassay conditions mortality in adult *H convergens* was just 18 %, demonstrating that different coccinellid species may vary greatly in their susceptibility to λ-cyhalothrin. In addition to species-specific differences, stage-specific differences also may be possible, e.g. a body of studies have shown that adult coccinellids are often less susceptible towards various insecticides compared to their immature stages (Koch, 2003). Kühne et al. (2002) reported possible high risks of λ-cyhalothrin spray drift deposits to adult *C. septempunctata*. By connecting λ-cyhalothrin spray drift deposit pattern with mortality data from laboratory testing, they identified areas within field margins with mortalities > 50 % for adult *C. septempunctata*. Drift pattern showed that ladybeetle

mortality > 50 % can occur at any distance within a field margin up to 5 m from the field edge. However, predicted mortalities were highly dependent on meteorological conditions during the application.

Corrected mortalities of *C. septempunctata* larvae exposed to top-leaf drift deposits on plants from either 1, 2, and 3 m from the field edge produced by insecticide application to fields 1 & 2 were high (> 46 %). Within 12 and 24 hours after exposure, mortalities did not show significant differences, so mortality risks for *C. septempunctata* larvae exposed to top-leaves at any distance from the field edge were the same, independently from the increasing field edge distance. This statistical insignificance is partly due to high variability in mortalities as a result of highly variable deposits. Three to 24 hours after exposure, mortalities caused by drift deposits from applications to field 3 in 2003 were again high on plants from within-crop and from 1 m distance (> 60 %). Significantly lower mortality rates were recorded on plants from 2 m and 3 m distance from the field edge. Particularly low mortalities on plants from 3 m (4 % after 24 hours) were in conformity with low deposits measured on leaf surfaces at 3 m distance from the field edge and reflected well the high percentage of measurements below detection level (75 %). In contrast, mortality rate of adult *A. colemani* exposed to deposits on plants from the same position within the weed strips was relatively high (26 %). This result contrasted with the findings of the current study showing higher susceptibility of *C. septempunctata* larvae to λ-cyhalothrin deposits compared to *A. colemani*. The patchiness of deposits may offer a potential explanation. *A. colemani* were exposed in groups of five within one clip cage, attaching this cage by chance to a highly contaminated leaf may cause the death of all or most parasitoids within this cage, a scenario that happened twice at 3 m distance thereby increasing mean mortality. *C. septempunctata* larvae were kept singly within cages, which were attached to neighbouring leaves of one collector plant. Only three times a cage was attached to deposits that caused the death of the caged larvae, whereas all other cages were by chance attached to uncontaminated leaf surfaces. This outcome again demonstrates the difficulties arising from the patchy drift deposition, which may lead to an under- as well as to an overestimation of risks.

2.4.4 Suitability of exposure bioassay methodology

Although deposit measurement and mortality assessment of test organisms could not be done on the same leaf but on closely adjoining leaves, high positive correlation coefficients proved the relationship between deposits of λ-cyhalothrin and mortality of

adult *A. colemani* as well as *C. septempunctata* larvae, thereby indicating the practicability of the method and its potential for further studies on the environmental impact of pesticide drift.

Compared to *A. colemani*, the relationship between deposits and mortality was stronger for *C. septempunctata* larvae. In contrast to the parasitoids, ladybeetle larvae were more susceptible towards λ-cyhalothrin and therefore showed a faster and more distinct reaction to deposits of λ-cyhalothrin, i.e. high mortalities of up to 100 % were observed when larvae were exposed to high deposits followed by a sharp decrease in mortalities at low deposits. Such a sharp decrease in mortalities was not shown in *A. colemani*, which showed a weaker "deposit-response" at high deposits due to lower susceptibility.

The influence of the delayed initial exposure of test organisms to deposits of λ-cyhalothrin may be relatively low since the product provides low photodegradation and high residual activity (Tomlin, 2003) as well as a relatively low rate of volatilization from leaves (anonymous, 2001).

2.4.5 Extrapolation of results from exposure bioassays to possible risks for A. colemani *and* C. septempunctata *in the field*

What information is extracted from exposure bioassays regarding possible mortality risks for individual adult *A. colemani* and *C. septempunctata* larvae in the field? On one hand, the exposure to dried insecticide deposits on leaf surfaces tends to underestimate risks. In the field, organisms may be highly endangered during the insecticide application, i.e. when they are directly hit by spray (drift) droplets or get in contact with fresh non-dry insecticide deposits. Oral uptake of contaminated food (e.g. aphids, honeydew) is another source of exposure to insecticides in the field (Longley & Stark, 1996). On the other hand, risks may be overrated since test organisms were forced to have continuous contact with insecticide contaminated leaf surfaces. In the field, aphid parasitoids (Jansen, 2001) as well as predatory ladybeetles (Singh et al., 2001) will search for hosts and prey and so come into contact with different or even no deposits on plant surfaces. Jansen (2001) observed just 11 % corrected mortality of adult *A. rhopalosiphi* exposed for 24 hours to wheat plants treated with a reduced rate of λ-cyhalothrin (5 g a.i./ha). Low mortality of wasps was explained by non-continuous contact to treated surfaces due to the parasitoids´ searching activity and their periodic flight behaviour. However, even short-time exposure to insecticides may affect insects.

Longley & Stark (1996) found a rapid uptake of the organophosphate insecticide diazinon by *A. ervi* within less than eight minutes of contact to deposits. Moreover, a full recovery of *A. rhopalosiphi* exposed to deltamethrin deposits just occurred when exposure period was less than five minutes (Longley & Jepson, 1997a). In the field, insects may avoid contact with plant parts contaminated with pesticides. In laboratory experiments, adult *C. septempunctata* spent less time on dimethoate-contaminated areas of broad beans compared to untreated parts, indicating an avoidance response (Singh et al., 2001). When exposed to treated wheat plants, *A. rhopalosiphi* displayed avoidance behaviour towards several fungicides (Jansen, 1999). Although not addressed in the current study, no evidence for repellent effects of λ-cyhalothrin on *C. septempunctata* or *A. colemani* was found. While checking for mortalities, test organisms were frequently found on the leaves. This finding seems to be in line with other studies. In extended laboratory tests with λ-cyhalothrin-treated plants there was no indication of repellent effects on *A. rhopalosiphi* (Jansen, 2001). Two pentatomid species were also not repelled by λ-cyhalothrin (Vandekerkhove & De Clerq, 2004).

In the present work, mortality of test organisms was the only endpoint measured. However, the impact of pesticides does not only result in death of non-target arthropods. Specimens that survive insecticide exposure may suffer from multiple sublethal effects such as reductions in longevity and fertility, changes in sex ratio, sterility, changes in searching, feeding or oviposition behaviour (Krespi et al., 1991; Provost et al., 2003; Stark & Banks, 2003; Stark et al., 2004a,b). Krespi et al. (1991) found a significant reduction in longevity of male and female *A. ervi* that had been exposed to λ-cyhalothrin deposits for one hour. In addition, females produced a significantly lower percentage of female offspring. However, a short-term exposure (10 minutes) seemed to have no sub-lethal effects on *A. ervi*. Exposure to a sublethal dose of λ-cyhalothrin affected the mobility of larvae of the ladybeetle *H. axyridis* (Provost et al., 2003). Both, the time spent moving and the velocity of larvae was significantly reduced by the insecticide.

The current work just looked at the toxicity of λ-cyhalothrin drift to one life stage of the test organisms. Field populations of *C. septempunctata* and *A. colemani* typically consist of several life stages, therefore possible drift effect questions on population dynamics cannot be answered empirically. The current study indicated that within-crop spray deposits as well as off-crop drift deposits of λ-cyhalothrin would cause a high degree of damage to *C. septempunctata* larvae. Mortality risks for the adult stage (LR_{50} for λ-cyhalothrin 1.74 ng/cm² (Kühne et al., 2002)) may also be high within-crop and at close distance from the field edge. Stark et al. (2004a,b) and Stark & Banks (2003)

stressed that population level effects of pesticides on non-target arthropods are considerably determined by population structures at the time of exposure to pesticides as well as by population growth rates. From a simulation model, Stark et al. (2004a) concluded that populations of *C. septempunctata* are more susceptible to pesticides than populations of the aphid parasitoid *Diaeretiella rapae* (M´Intosh) and the pea aphid *Acyrtosiphon pisum* Harris due to their lower population growth rate, their longer generation time and their higher number of life stages compared to parasitoids and aphids. Therefore, as a consequence of the current study, the potential risks for populations of *A. colemani* from λ-cyhalothrin may be less dramatic compared to *C. septempunctata* due to their higher intrinsic rate of increase (Stark et al., 2004a) and the lower susceptibility of adult *A. colemani* to λ-cyhalothrin. In addition, λ-cyhalothrin seems to have no negative effect on emergence of adult parasitoids from the mummy stage (Krespi et al., 1991).

In a second part of this study, the effects of insecticide drift on the population dynamics of non-target arthropods (parasitoids and foliage dwelling predators) and target pests (aphids) were analysed; analyses were based on different sampling and monitoring methods, thereby recording different life stages. This approach includes differential susceptibility often found among life stages within a species (e.g. Krespi et al., 1991; Longley & Jepson, 1997b). In addition, population recovery and reimmigration processes are considered which may compensate, to a certain degree, for pesticide effects on individual specimens.

Results from the current drift deposit measurements and the exposure bioassays are essential for a detailed interpretation of impacts on population levels found in the field.

3. *Effects of λ-cyhalothrin drift into field margin habitats on population dynamics of aphids and their natural enemies*

3.1 INTRODUCTION

In intensively managed agricultural landscapes field margins are an important semi-natural habitat type having essential environmental and conservational functions. These habitats, usually less than one meter to a few meters wide, are linear structures running along agricultural fields, thereby forming networks of field margins amounting to a total length of several thousands of kilometres, for instance in Germany or Finland (Welling, 1987; Kühne et al., 2000; Helenius & Bäckman, 2004).

Past research has shown enhanced density and species richness of different beneficial arthropod communities in field margin habitats (MacLeod, 1999; Thomas & Marshall, 1999; Sutherland et al., 2001a; Denys & Tscharntke, 2002; MacLeod et al., 2004). For important natural enemies of cereal aphids, such as soil and plant dwelling predators, e.g. ground beetles (Carabidae), ladybeetles (Coccinellidae) spiders (Araneae), lacewing larvae (Chrysopidae), and hoverfly larvae (Syrphidae) as well as aphid parasitoids (Braconidae), field margins can act as permanent habitats (Levie et al., 2000; Sigsgaard, 2002; Nyfeller & Sunderland, 2003). By providing food (e.g. pollen, nectar, and alternative prey) or hosts, field margins can be temporary refuges after harvest or tillage and are also known to be used as overwintering sites by a variety of beneficial arthropod species (Varchola & Dunn, 2001; Lemke & Poehling, 2002; Frank & Reichhart, 2004; MacLeod et al., 2004). As linear features, these habitat types can act as corridors for the movement of (beneficial) arthropods between crops and between crop and off-crop (Joyce et al., 1999; Marshall & Moonen, 2002). Moreover, arthropods are thought to disperse from field margin habitats into adjacent crops (e.g. Bowie et al., 1999; Denys & Tscharntke, 2002; Langer & Hance, 2004; Pickett et al., 2004). As a result of these functions, the presence of field margins can increase the abundance and species richness of beneficial arthropods in the adjacent crops, as it has been shown for spiders (Huusela-Veistola, 1998), carabid beetles (e.g Lee et al., 2001), hoverflies (White et al., 1995; Bowie et al., 1999), or aphid parasitoids (Langer & Hance, 2004; Levie et al., 2004).

Pesticides that are regularly applied to intensively managed crops do not only affect the target pests within the crop but can also have a negative impact on beneficial and indifferent arthropod species, which has been expounded by a bulk of studies (e.g. Longley et al., 1997a; Holland et al., 2000; Jansen, 2000; Candolfi et al., 2004; many more). Within field margin habitats pest and beneficial arthropods may be protected at

the time of pesticide application and surviving individuals might contribute to repopulation by reinvasion from field margins into the crop after insecticide applications (Longley et al., 1997a; Holland et al., 1999; Holland et al., 2000; Lee et al., 2001). Thereby, field margin habitats can buffer the detrimental impact of insecticide applications on arthropod populations in adjacent fields. However, this important function of field margins is endangered due to their close proximity to agricultural operations. The most relevant route of contamination of terrestrial off-crop areas is pesticide spray drift (Candolfi et al., 2001; Koch et al., 2003), i.e. the physical movement of pesticide droplets through the air away from the target area to non-target off-crop areas at the time of the application (Ganzelmeier et al., 1995). Drift is unavoidably associated with the application of plant protection products (Kaul et al., 2001a) and can affect non-target organisms directly by contact with airborne particles during application or indirectly by contact with spray deposits on plant or soil surfaces or by the ingestion of contaminated food (e.g. Longley & Stark, 1996).

So far only limited data are available regarding the effects of insecticide drift on population dynamics of terrestrial non-target arthropods within field margin habitats. Kühne et al. (2002) estimated effects of insecticide (λ-cyhalothrin) drift on population dynamics of various arthropod groups within a field margin. Their study showed that, depending on the extent of drift into the off-crop, total mite populations as well as total numbers of arthropods might be significantly reduced by insecticide drift up to a distance of 5 m from the field edge. A significant decline in numbers of grasshoppers was detected at 1 m from the sprayed crop. Densities of all other arthropod groups under investigation were not reduced by λ-cyhalothrin drift. Holland et al. (2000) found that insecticide (dimethoate) drift from treated wheat fields caused a significant decline in aphid parasitoid (*Aphidius* spp.) as well as spider (Linyphiidae) abundance within a 6 m wide unsprayed buffer zone; drift of the same product also caused a decrease in total arthropod numbers within the buffer zone (Holland et al., 1999).

This study investigated the effects of insecticide drift on the population dynamics of cereal aphids and selected groups of their natural enemies, i.e. plant dwelling predators of the families Coccinellidae, Chrysopidae, and Syrphidae and cereal aphid parasitoids of the family Braconidae. The main objectives of this work were (1) to assess the impact of insecticide drift into field margin strips bordering on winter wheat fields on the population development of aphids and their natural enemies, and (2) to estimate the influence of drift-contaminated and drift-protected field margins on within-crop population recovery through immigration following the insecticide treatment.

3.2 MATERIAL AND METHODS

3.2.1 Experimental design

The study was carried out on three intensively farmed winter wheat fields (approximately 3.8, 6.6 and 12 ha) near Pattensen, 25 km south of Hannover, Germany. The sites were privately managed. The study area is characterised by its intensive farming practise due to fertile clay-loess soils. The landscape is flat and structurally "poor", i.e. proportions of small landscape elements like field boundaries, hedges, and woodlots are insufficient (BBA, 2002b). The actual percentage of small landscape elements in the study area amounts to 9.5 %; to achieve the desired minimal requirement of 12.8 %, further 181 ha of small landscape elements are required (BBA, 2004). Parallel to the lane (i.e. the driving direction of the field sprayer) 3 m broad sown weed strips, sown with a wild flower mixture (modified according to Nentwig, 1992), were established along one edge of each wheat field (Fig. 1). The seed mixture consisted of 22 species of flowering plants (Tab. 1) attractive to several groups of beneficial arthropods (Nentwig, 1992).

Tab. 1. Seed mixture composition.

Scientific name	English name	Amount [g/ha]
Achillea millefolium L.	Common Yarrow	20
Agrostemma githao L.	Common Corncockle	600
Anthemis tinctoria L.	Yellow Chamomile	20
Centaurea cyanus L.	Cornflower	500
Centaurea jacea L.	Radiant Cornflower	200
Chrysanthemum leucanthemum L.	Oxeye Daisy	80
Cichorium intybus L.	Chicory	120
Dipsacus fullonum L.	Teasel	2
Echium vulgare L.	Viper´s Bugloss	200
Fagopyrum esculentum Moench	Buckwheat	7845
Hypericum perforatum L.	St John´s Wort	60
Legousia speculum-veneris (L.)	Venus´ Looking Glass	30
Malva moschata L.	Musk Mallow	20
Malva sylvestris L.	Common Mallow	60
Melilotus albus Medik.	White Melilot	20
Onobrychis viciifolia Scop.	Sainfoin	600
Origanum vulgare L.	Marjoram	60
Pastinaca sativa L.	Wild Parsnip	80
Silene alba (Mill.)	White Campion	100
Tanacetum vulgare L.	Tansy	3
Verbascum densiflorum Bertol.	Torch Weed	50
Verbascum lychnitis L.	White Mullein	30

In the sown weed strips, transects of wheat were established at distances of 1 and 2 m from the field edge in order to estimate densities of cereal aphids and aphid specific natural enemies within the field margin strips. As “trap plants”, wheat tillers allowed a systematic estimation of natural population densities. Length of field margin strip 1 bordering on field 1 was 230 m, length of strip 2 bordering on field 2 was 234 m and length of strip 3 bordering on field 3 was 419 m. Field margins and adjacent wheat areas were divided into 16 plots of equal size (approximately 52 m x 25 m), providing four experimental field plots each on field 1 & 2 and eight plots on field 3 (Fig. 1). A control and a drift treatment were performed; these were randomly distributed among the 16 field plots (Fig. 1).

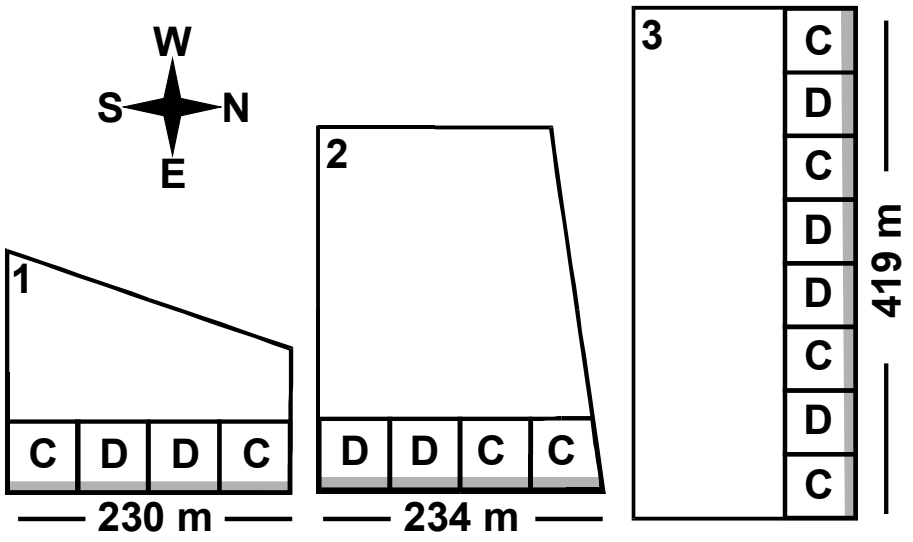

Fig. 1. Experimental layout (not to scale). Allocation of control (C) and drift (D) field plots on the three experimental wheat fields. From left to right: field 1 (3.8 ha), field 2 (6.6 ha) and field 3 (12 ha). Grey area: field margin strips; white area: wheat.

3.2.2 Insecticide application

In both years the synthetic pyrethroid Trafo® (active ingredient λ-cyhalothrin), widely used in Europe to control aphids in cereals (anonymous, 2000a; Kühne et al., 2002), was applied at its respective recommended rate (2002: Trafo liquid, Urania: 10 g a.i./ha; 2003: Trafo WG, Syngenta: 7.5 g a.i./ha). In order to provoke drift, detectable wind should preferably blow at an angle of 90° to the field margin strips during insecticide application. Since strips 1 & 2 were west facing and strip 3 was south facing

(Fig. 1), in each year insecticide application to wheat fields 1 & 2 was done on the same day and application to field 3 was done on a separate day. The insecticide was applied at the middle/end of wheat flowering (BBCH 65/69) on 14 June (field 1 & 2) and 16 June (field 3) in 2002 and on 20 June (field 3) and 21 June (field 1 & 2) in 2003. Applications were done using a conventional tractor mounted field sprayer (15 m boom) equipped with multirange flat spray nozzles LU 120 03, i.e. a standard, non low-drift nozzle type. Nozzle spacing was 50 cm and boom height above the canopy was 50 cm. A water volume of 200 l/ha was achieved with an operating pressure of 3.6 bar and a forward speed of 7.2 km/h (2002) and 3 bar and 6.4 km/h (2003), respectively. A control and a drift-treatment were performed. During insecticide application control weed strips were covered with polythene sheets to prevent contamination due to insecticide drift, whereas drift weed strips were left uncovered. Each treatment was replicated eight times. A fluorescent tracer was added to the spray liquid; drift deposits into the field margin strips were measured using broad bean, *Vicia faba* L., as natural drift collectors (cf. 2.2.3, page 10 et seq.).

3.2.3 Arthropod monitoring

Two separate methods of estimating arthropod population densities were conducted weekly. (1) Visual counts were made along the sown wheat transects within the field margin strips at 1 and 2 m from the field edge and along transects at distances of 5 and 25 m from the field edge into the wheat (Fig. 2). At each monitoring distance 50 wheat tillers were selected randomly (400 tillers per distance and replicate at each assessment date, i.e. a total of 3,200 tillers) and inspected for the three cereal aphid species *Rhopalosiphum padi* (L.), *Metopolophium dirhodum* (Walker) and *Sitobion avenae* (F.), for aphid mummies and for the different stages (egg, larva, adult) of the plant-dwelling predatory groups Chrysopidae, Coccinellidae, and Syrphidae. In both years visual counts were conducted over a six-week period; in 2002 counting started on 12 June and in 2003 on 16 June.

(2) To estimate population densities of leaf dwellers and flying insects standardised sweep netting was conducted. Sweep samples consisted of 25 (2002) and 50 (2003) sweeps with a 30 cm diameter sweep net. Samples were taken along four linear transects in the centre of each plot, i.e. within the field margin strips (1.5 m from the field edge) and at 4 and 24 m into the wheat (Fig. 2). While taking 25 sweeps a distance of approx. 25 m was covered. In 2003 the 25 m transect was walked in both directions, displacing the way back by one step. In 2002 sweep netting started on 11

June and in 2003 on 17 June; it was conducted over a 4.5-week period in 2002 and over a 5.5-week period in 2003. On all sample dates, sweep sampling was started after 9 a.m. to avoid early morning dew. If the foliage is wet small insects may stick to the inside of the sweep net bag making it very difficult to remove them. Sampling was usually completed by 1 p.m.. Since sweep netting is ideally conducted when foliage is dry and when wind speed is below 2 m/s (cf. 6.3, page 168 et seqq.), it was not always possible to conduct sweep sampling at regular time intervals, e.g. every 7th day.

In 2002 sweep netting was terminated earlier, since three strong rainfall events in mid July (20, 23, and 72 mm rain/day) caused lodging, i.e. wheat fields were laying flat, which impeded sweep netting.

Catches were stored in ethanol (70 %) prior to identification. Specimens of the predatory groups Chrysopidae, Coccinellidae, and Syrphidae as well as braconid aphid parasitoids were identified to family level (larvae) and to species level (adults), respectively, and sexed. Identification to species followed Schaefer (2002) for chrysopids, Klausnitzer & Klausnitzer (1997) for coccinellids, Stubbs & Falk (1983) for syrphids, and Starý (1973) and Powell (1982) for cereal aphid parasitoids. Due to their similarity, which makes them difficult to separate, *Aphidius rhopalosiphi* DeStefani-Perez and *Aphidius uzbekistanicus* Luzh. were pooled into *A. uzbekistanicus*-group (Powell, 1982; Langer, 2001). Of each species identified one reference exemplar was kept.

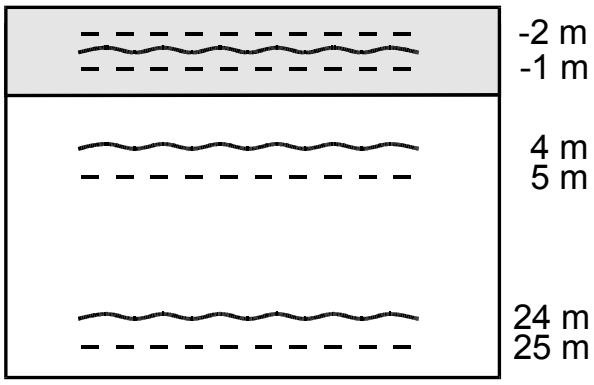

Fig. 2. Sample positions in one replicate field plot at different distances from the field edge (not to scale). Dashed lines: transect counts; undulated lines: sweep net samples; grey area: field margin strip; white area: wheat.

3.2.4 Data analysis

Two separate analyses were performed: (1) analysis of drift effects on population dynamics of insects in field margin strips and (2) analysis of within-field reimmigration/recovery trends in insect populations following the insecticide application.

(1) Analysis of drift effects: To analyse the impact of insecticide drift on arthropod population densities within the field margin strips and to determine recovery trends over time post-treatment count/catch data at each sample position were subtracted from the pre-treatment count/catch data to yield a "difference-value" (Longley et al., 1997a; Holland et al., 2000). Difference values of the drift-treatment at each distance from the field edge were compared with difference values from the equivalent control plot positions using the independent-samples t-test. If the variances were unequal, Satterthwaite's t-test for unequal variances was used.

Statistical analysis of drift effects was restricted to taxa, which occurred in sufficient densities (i.e. mean ≥ 1 stage per 50 tillers and sweep sample, respectively) within the field margin strips either prior to the insecticide application or on the first post-treatment monitoring date to ensure that statistical tests have adequate power to detect true drift effects. Statistical analysis was done at functional group level (i.e. separately for developmental stages of (cereal) aphids, cereal aphid parasitoids, chrysopids, aphidophagous coccinellids, and aphidophagous syrphids) and, wherever applicable, at species level.

(2) Analysis of within-field population recovery: Spatial population recovery over time was estimated by nonparametric rank analysis of variance, Anova-type statistic (ATS) (Brunner & Munzel, 2002), using the distance from field edge as fixed factor and the pre-treatment densities at each sample position as covariate. Subsequent to an insecticide application, within-field recovery of arthropod populations is generally thought to be composed of recovery that is mediated by reimmigration from untreated surrounding habitats and recovery through reproduction by surviving specimens (e.g. Longley et al., 1997a). Since both components of recovery could not be separated in the current study, the covariate was included in the model for increased precision in determining the effect of pre-treatment densities on the post-treatment differences in population densities across field plots. Comparisons were made between arthropod densities within the field margin strip and at 5 and 25 m (count data) and 4 and 24 m (sweep net data) into the wheat, respectively, for drift and control treatment separately.

To estimate recovery trends based on count data, the mean values of densities estimated at 1 and 2 m from the field edge were used. To compensate for multiple comparisons the p-value was adjusted to 0.0167 using Bonferroni correction.
Analysis was done at functional group level (i.e. separately for developmental stages of (cereal) aphids, cereal aphid parasitoids, chrysopids, aphidophagous coccinellids, and aphidophagous syrphids) and, wherever applicable, at species level.
Data analysis was done using the programme SAS 8.02 (SAS, 2001).

3.2.5 Meteorological data

Meteorological data were received from a nearby weather station (1 km) at the Ruthe field station of the University of Hannover. Wind speed and wind direction at the time of spraying were recorded at 2 m height at the experimental site using a stationary anemometer (Lambrecht, Göttingen, Germany) and a portable hand wind gauge (ELV Elektronik, Leer, Germany).

3.3 RESULTS

3.3.1 Meteorological data

Figure 3 shows the average daily temperature, the 30-year long-term mean temperature, and the total daily precipitation for June and July 2002. Monthly average temperatures were 1.6°C (June) and 0.9°C (July) above the 30-year mean. In June precipitation was slightly below average, whereas July was a very wet month with a monthly rainfall total of 166 mm, which was approximately 2.6 fold above average. The highest rainfall was recorded on 17 July (72 mm). One day subsequent to the insecticide application in fields 1&2, 3.3 mm of rain fell. On three out of the 11 following days rainfall was recorded (< 1.8 mm/day). From the end of June to late July precipitation increased (Fig. 3).

Figure 4 shows the average daily temperature, the 30-year long-term mean temperature, and the total daily precipitation for June and July 2003. Monthly average temperatures were 3.8°C (June) and 3.2°C (July), respectively, above the 30-year mean. Precipitation was below average throughout June and July, respectively. In the first week subsequent to the insecticide application in the wheat fields, no rain was recorded, except for 8 mm on day two and three post-spray, respectively.

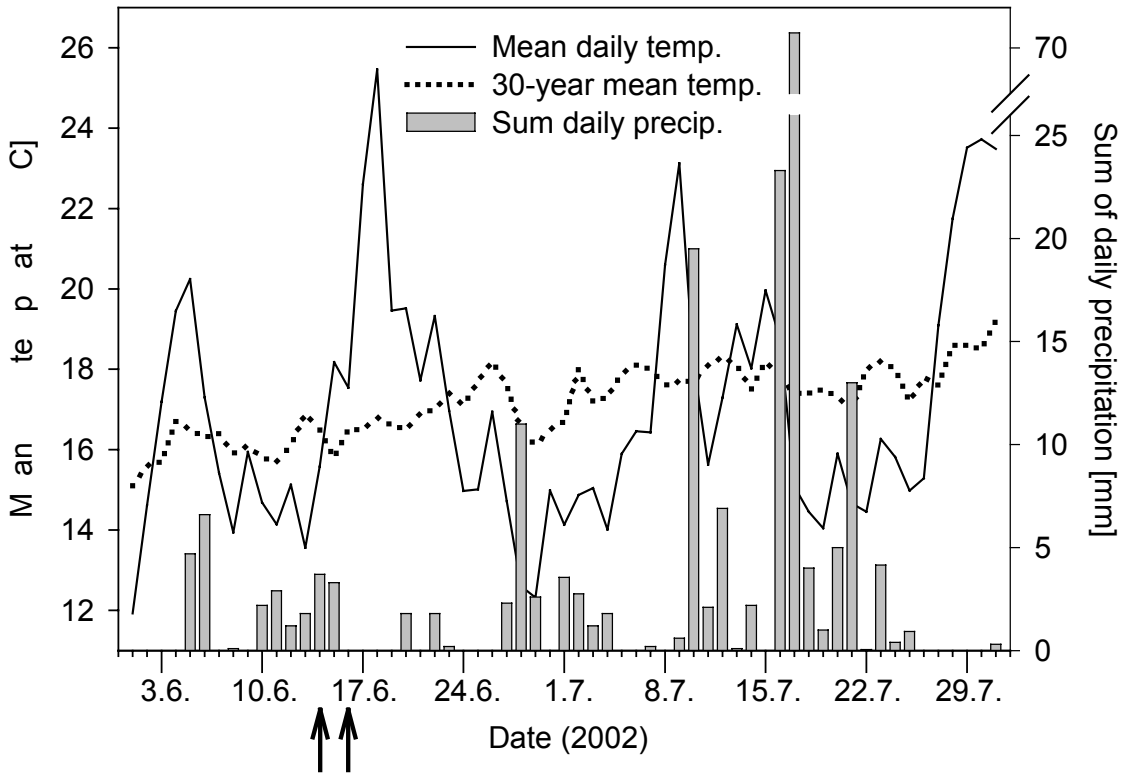

Fig. 3. Meteorological data for the period 1 June to 31 July 2002. Arrows indicate date of insecticide applications (14.6. & 16.6.2002).

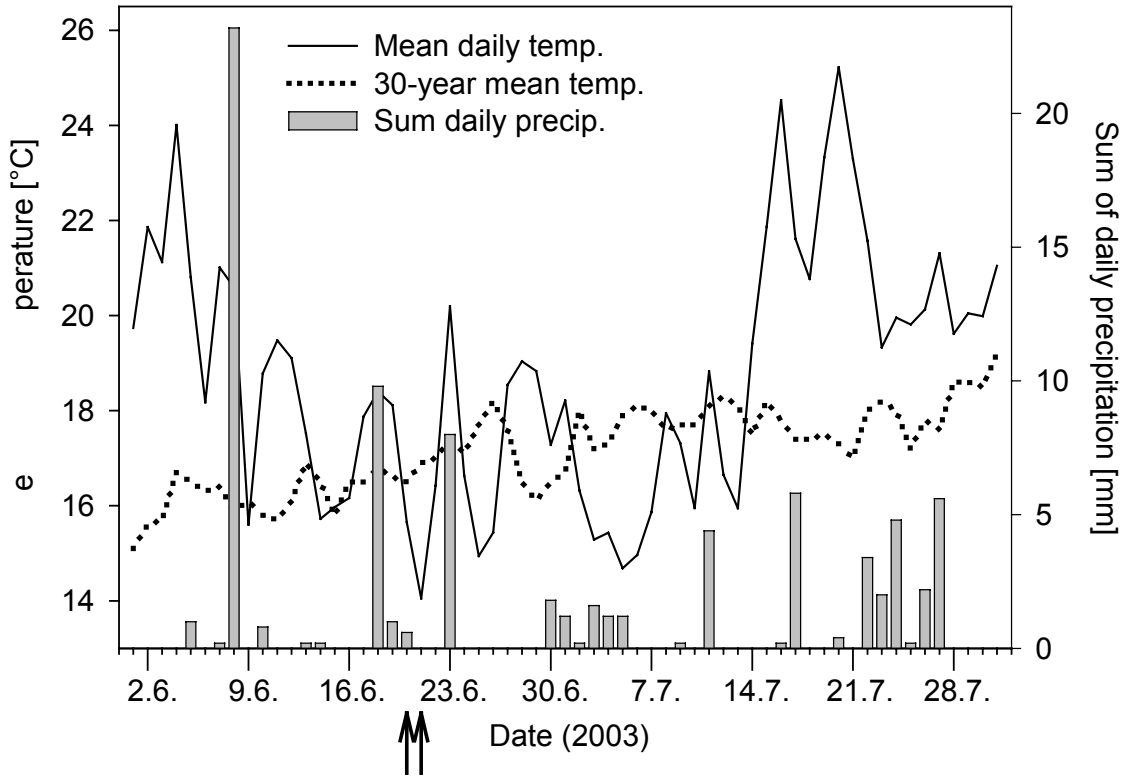

Fig. 4. Meteorological data for the period 1 June to 31 July 2003. Arrows indicate date of insecticide applications (20.6. & 21.6.2003).

3.3.2 Spray drift deposits on plant surfaces

Table 2 lists deposit means of λ-cyhalothrin on individual leaves of broad bean plants that had been exposed during the insecticide application within the field and within the field margin strips at distances of 1, 2, and 3 m from the field edge. Detailed information on the deposit measurement procedure and on the drift deposition on leaf surfaces are given in section 2.2.3, page 10 et seq..

Tab. 2: Mean deposits of λ-cyhalothrin [ng/cm²] ± standard errors on leaf surfaces of broad beans exposed to insecticide spray within the wheat fields and to insecticide drift within field margin strips at 1, 2, and 3 m distance from the field edge in 2002 and 2003.

Position of leaf sample		2002	2003
ear-height	field	6.07 ± 1.83	7.52 ± 1.92
	1 m	0.36 ± 0.06	0.66 ± 0.15
	2 m	0.12 ± 0.03	0.40 ± 0.12
	3 m	0.06 ± 0.01	0.17 ± 0.04
ground-level	field	1.22 ± 0.61	1.47 ± 0.34
	1 m	0.61 ± 0.12	0.63 ± 0.14
	2 m	0.11 ± 0.03	0.15 ± 0.04
	3 m	0.04 ± 0.01	0.07 ± 0.02

3.3.3 Insects observed during visual counts

In 2002, cereal aphids were the most abundant taxa found on wheat tillers, with a total count of 35,778 (63 % *R. padi*, 33 % *M. dirhodum*, 4 % *S. avenae*). In addition, a total of 1,180 developmental stages of syrphids (69 % eggs, 26 % larvae, 5 % pupae), 863 aphid mummies, 141 developmental stages of chrysopids (88 % eggs, 11 % larvae, 1 % pupae), and just 24 developmental stages of coccinellids (67 % adults, 21 % larvae, 13 % eggs) were recorded during visual counts.

In 2003, cereal aphids were again the most abundant taxa, with a total count of 45,018 (63 % *R. padi*, 19 % *S. avenae*, 18 % *M. dirhodum*). A total of 976 developmental stages of chrysopids (88 % eggs, 11 % larvae, 1 % pupae), 452 developmental stages of syrphids (50 % eggs, 42 % larvae, 8 % pupae), 361 aphid mummies, and 169

developmental stages of coccinellids (57 % eggs, 27 % larvae, 15 % adults, 1 % pupae) were counted on wheat tillers.

3.3.4 Insects captured by sweep netting

In 2002 aphids were the most abundant taxa captured by sweep netting, with a total number of 26,533 (92 % apterous, 8 % alate aphids). Additionally, a total of 1,137 developmental stages of syrphids (97 % adults (70 % *Melanostoma mellinum* (L.), 17 % *Episyrphus balteatus* (DeGeer), 6 % *Eupeodes corollae* (Fabricius), others < 5 %), 3 % larvae), 892 cereal aphid parasitoids (47 % *A. uzbekistanicus*-group, 41 % *Aphidius picipes* (Nees), others ≤ 5 %), and 238 developmental stages of chrysopids (72 % larvae, 28 % adult *Chrysoperla carnea* (Stephens)) were collected. Numbers of coccinellids in sweep net samples were very low (six adults (five *Coccinella septempunctata* L., one *Propylea quatuordecimpunctata* (L.)) and two larvae).

In 2003 aphids were again the most frequently caught taxa, with a total number of 58,882 (90 % apterous, 10 % alate aphids). A total of 2,240 developmental stages of chrysopids (60 % larvae, 40 % adult *C. carnea*), 1,613 developmental stages of syrphids (81 % adults (46 % *E. balteatus*, 21 % *E. corollae*, 16 % *Sphaerophoria scripta* (L.), 15 % *M. mellinum*, others ≤ 1 %) 17 % larvae, 2 % pupae), 961 cereal aphid parasitoids (82 % *A. uzbekistanicus*-group, others ≤ 6 %), and 154 developmental stages of coccinellids (79 % larvae, 21 % adults (60 % *C. septempunctata*, 27 % *P. quatuordecimpunctata*, 10 % *Adonia variegata* (Goeze), 1 % *Coccinella undecimpunctata* L.)) were identified from sweep samples.

3.3.5 Effect of λ-cyhalothrin drift on the population development of aphids and their natural enemies

Count data 2002

In 2002 the three cereal aphid species (*R. padi*, *S. avenae,* and *M. dirhodum*), aphid mummies, and syrphid eggs occurred in sufficient densities (cf. 3.2.4) on wheat tillers to allow reasonable statistical analysis of drift effects. Densities of syrphid larvae and pupae, developmental stages of chrysopids, and coccinellids were low during the whole study period, with a mean of < 1 stage per 50 tillers.

Lambda-cyhalothrin drift into field margin strips caused a significant decline in densities of ***R. padi*** at 1 m distance from the field edge (t-test: df = 14, t = -2.21, p = 0.044)

compared to the control. The same trend was observed for **total cereal aphid** densities (t-test: df = 14, t = -1.91, p = 0.068) (Fig. 5a & b). At 2 m distance from the field edge no significant effects of λ-cyhalothrin drift on the population development of *R. padi* (t-test: df = 14, t = -1.36, p = 0.196) and total cereal aphids (t-test: df = 14, t = -1.45, p = 0.168) were detected. Drift effects were transitory, on 26 June (10/11.5 days p.a.) no effects on densities of *R. padi* and total cereal aphids at 1 m distance from the field edge were detected (Fig. 5a & b).

From the second post-treatment count (26 June) densities of total cereal aphids and *R. padi* in the field margin strips sharply decreased both in control and drift-treatment. Until harvest, populations did not build up again (Fig. 5a & b).

Insecticide drift into field margin strips did not significantly influence the population development of the two other cereal aphid species, ***S. avenae*** and ***M. dirhodum***. No adverse effects of insecticide drift on population densities of *M. dirhodum* were detected; following the insecticide application numbers increased in both control and drift treatment. From 26 June an overall decrease in densities of *M. dirhodum* was observed (Fig. 5c).

Numbers of *S. avenae* in the drift contaminated field margins decreased subsequent to the application of λ-cyhalothrin at both 1 and 2 m from the field edge, but populations built up again and exceeded the pre-treatment levels on 26 June. From 9 July densities of *S. avenae* declined in both control and drift-treatment (Fig. 5d).

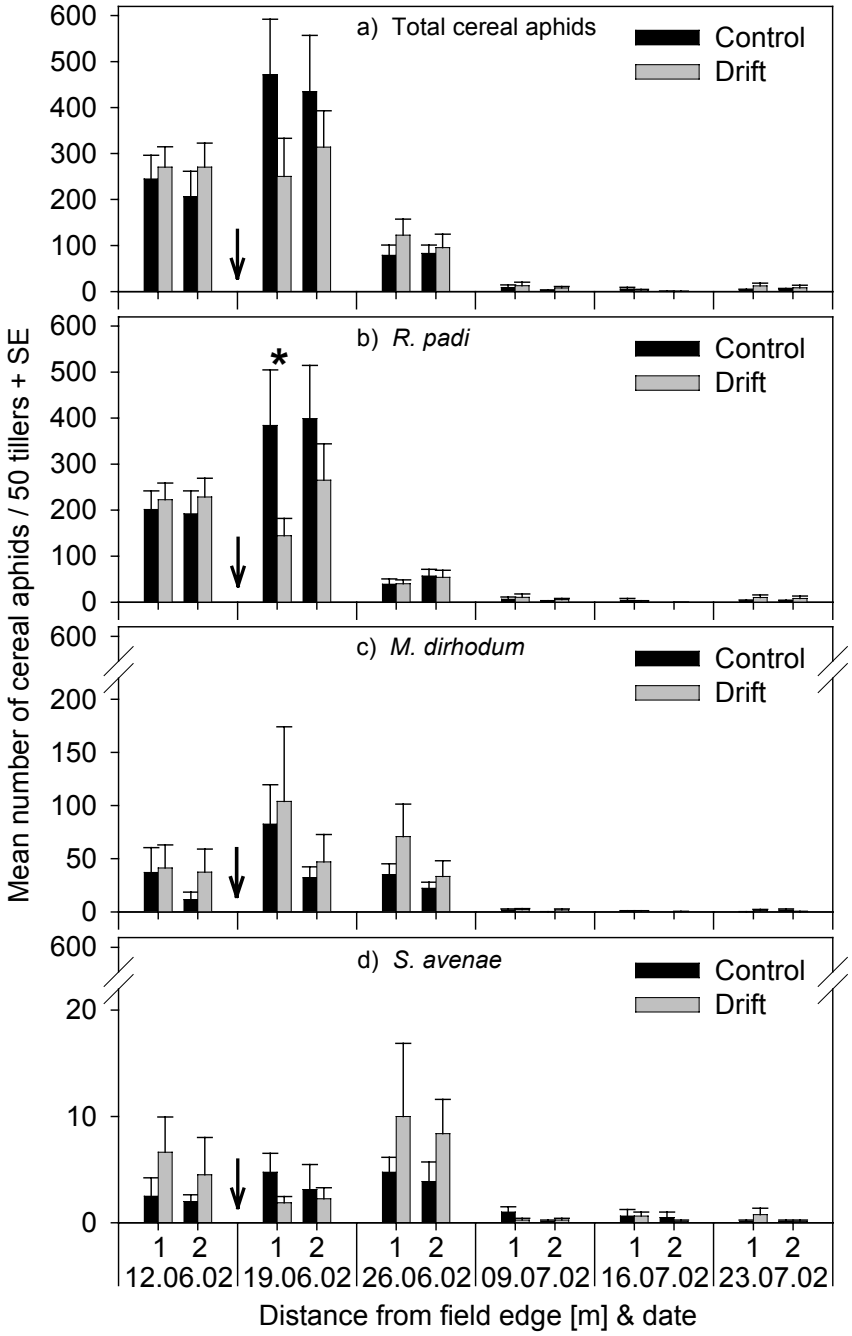

Fig. 5. Mean numbers (+ SE) of total **cereal aphids** (a), ***R. padi*** (b), ***M. dirhodum*** (c), and ***S. avenae*** (d) per 50 tillers within the field margin strips at 1 and 2 m distance from the field edge before and after the application of λ-cyhalothrin to wheat fields in 2002. Asterisks indicate statistically significant differences ($p < 0.05$) in population changes between control and drift-treatment. The arrow indicates date of insecticide application. Result t-test (*R. padi*, 19.06.02, 1 m): df = 14, t = -2.21, p = 0.044.

Insecticide drift into field margin strips seemed not to influence densities of **mummified aphids**. On almost all pre- and post-application dates differences in mean numbers of mummies between control and drift-treatment were marginal (Fig. 6a).

When compared with the control, λ-cyhalothrin drift had no significant effect on the numbers of **syrphid eggs**. Following the application, densities initially increased in both control and drift contaminated field margin strips, as did aphid densities (cf. Fig. 5a).

Along with the cereal aphids, numbers of both, mummified aphids and syrphid eggs, decreased from 9 July (Fig. 6a & b).

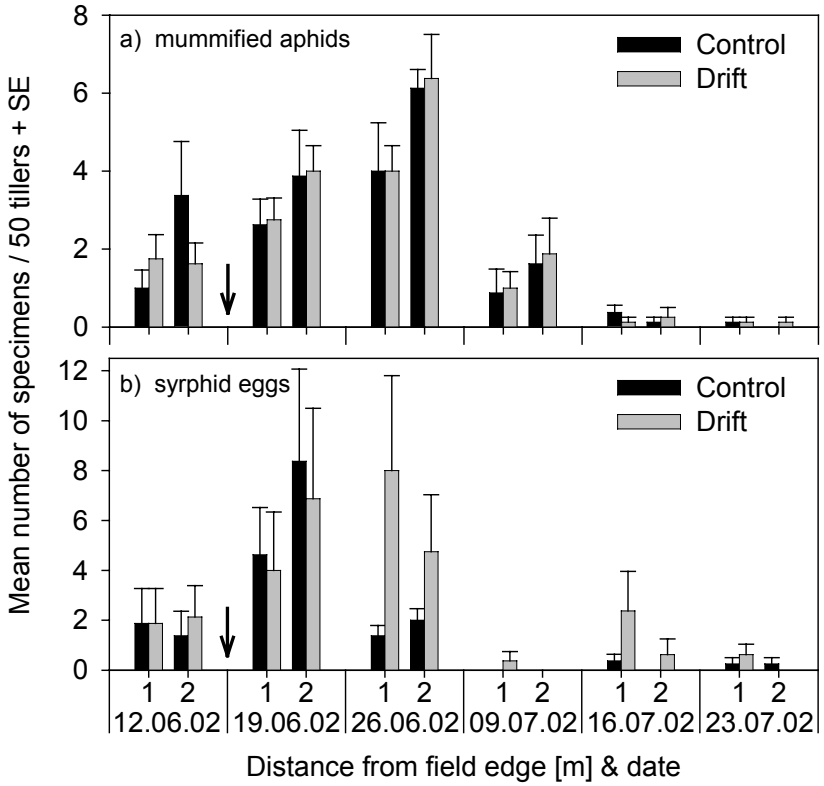

Fig. 6. Mean numbers (+ SE) of **mummified aphids** (a) and **syrphid eggs** (b) per 50 tillers within the field margin strips at 1 and 2 m distance from the field edge before and after the application of λ-cyhalothrin to wheat fields in 2002. The arrow indicates date of insecticide application.

Sweep net data 2002

By sweep netting apterous and alate aphids, cereal aphid parasitoids, and syrphid flies were caught in sufficient numbers (cf. 3.2.4) for reasonable statistical testing. In addition to analysis at functional group level, analysis was conducted at species level for cereal aphid parasitoids belonging to the *A. uzbekistanicus*-group and for the syrphid species *M. mellinum*. Adults and larvae of coccinellids and chrysopids as well as syrphid larvae were sporadically captured over the 2002 sweep catch-period; numbers of most stages were low (mean of < 1 stage per 25 sweeps at almost all dates).

Insecticide drift into field margin strips had a negative, although statistically insignificant, effect on population densities of **apterous aphids**. The first post-treatment sweep catch (20 June) revealed an increase in densities compared to pre-treatment catches in both control and drift-treatment strips. However, the increase in the control (579 ± 154 SE aphids/25 sweeps) tended to be higher compared to the increase in the drift contaminated field margin strips (226 ± 91 SE aphids/25 sweeps) (t-test: $df = 14$, $t = -1.97$, $p = 0.068$). This effect was transitory; although sweep samples from 28 June indicated that mean numbers of apterous aphids were higher in control field margins compared to drift contaminated margins (Fig. 7a), no significant differences in population changes between control and drift treatment were observed ($p = 0.258$). Populations of apterous aphids declined from 28 June (Fig. 7a).

Subsequent to the application of λ-cyhalothrin in wheat fields, numbers of **alate aphids** initially increased in both, control and insecticide drift-contaminated field margins (Fig. 7b). Overall, no significant differences in the population development of winged aphids between both treatments were detected throughout the sampling period. As apterous aphids, alate aphids also declined from 28 June (Fig. 7b).

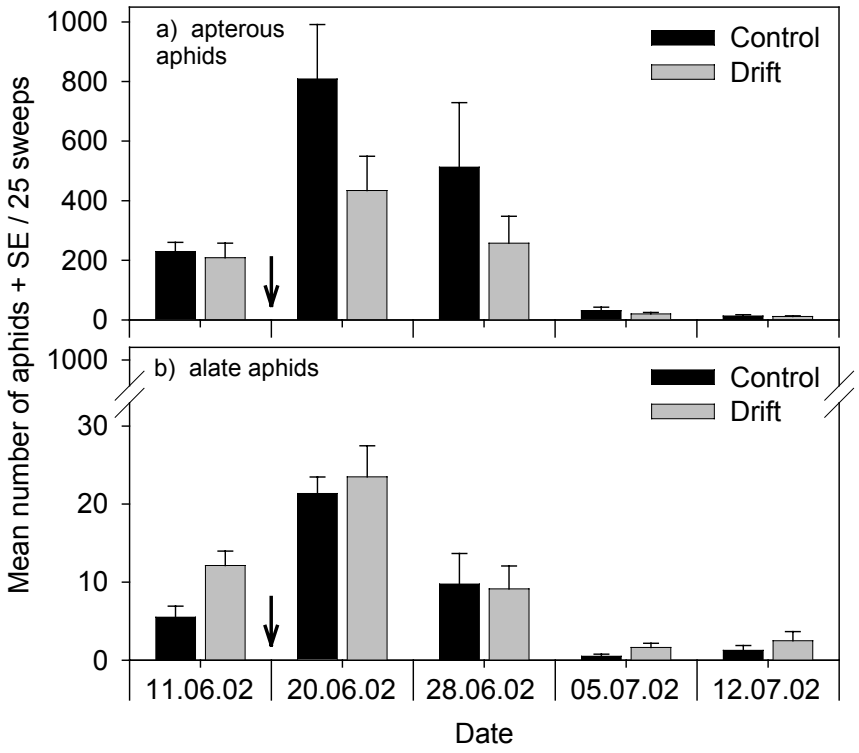

Fig. 7. Mean numbers (+ SE) of **apterous** (a) and **alate** (b) **aphids** per 25 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2002. The arrow indicates date of insecticide application.

Numbers of **cereal aphid parasitoids** in pre-treatment catches (11 June) were very low. On average, less than one parasitoid was caught by 25 sweeps (Fig. 8a). Following the application, numbers increased in both control and insecticide drift-contaminated field margin strips. On 20 June, a higher, though statistically insignificant, increase in numbers of total cereal aphid parasitoids was noticed in control strips compared to drift-strips (t-test: df = 14, t = -1.43, p = 0.175). However, statistical analysis on species-level did not affirm this trend. No indications for differences in the population development of the most abundant cereal aphid species-group, ***A. uzbekistanicus*-group**, between control and drift field margins was found (t-test: df = 14, t = -0.70, p = 0.493) (Fig. 8b). On 28 June, low numbers of cereal aphid parasitoids (mean < 1 per sweep sample) were captured by sweep netting. This weak capture efficacy was related to the relatively strong wind (mean 4.5 m/s) when sweep netting was conducted (see also 5.3.3, page 143 et seqq.). Due to the limited time frame of the study and the bad weather forecast, sampling was done despite the unfavourable conditions. On all other sampling dates wind speed was lower (< 3 m/s). In control field margins, total cereal aphid parasitoids as well as the *A. uzbekistanicus*-group peaked on 5 July and then decreased, whereas the numbers captured in the drift

field margins on 5 and 12 July remained relatively constant. No significant differences in population dynamics of total cereal aphid parasitoids and the *A. uzbekistanicus*-group between control and drift-treatment were recorded on 5 and 12 July (Fig. 8b).

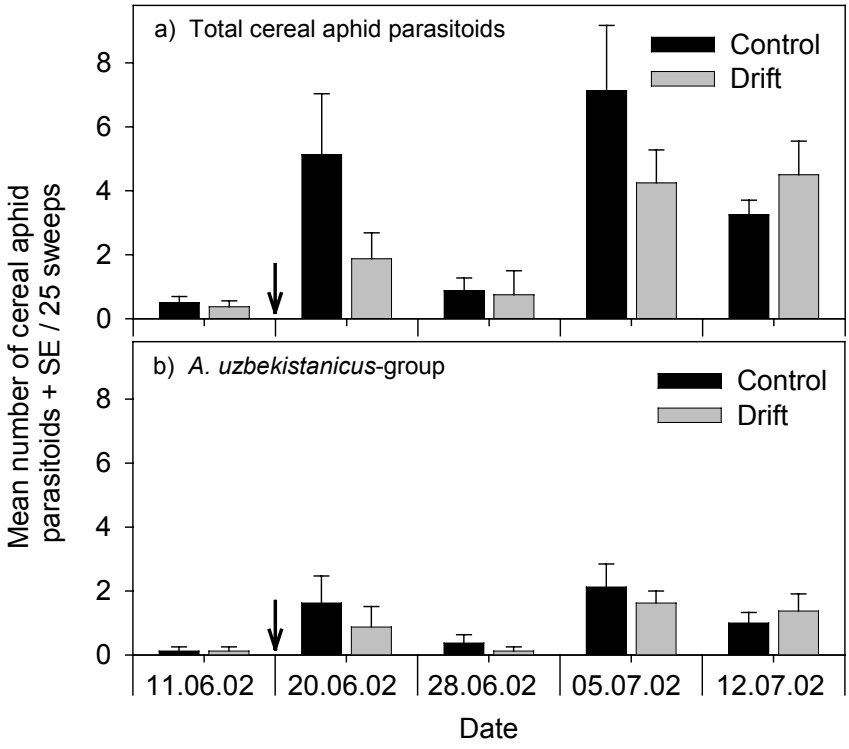

Fig. 8a & b. Mean numbers (+ SE) of total **cereal aphid parasitoids** (a) and the ***A. uzbekistanicus*-group** (b) captured per 25 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2002. The arrow indicates date of insecticide application.

Following the application of λ-cyhalothrin to wheat fields, numbers of total **syrphid flies** and the species ***M. mellinum*** increased compared to pre-treatment densities in both, control and insecticide drift-contaminated field margin strips (Fig. 9a & b). Densities increased with time, highest numbers of syrphids were captured on the last sampling date (12 July). Overall, no significant differences in the population dynamics of both total syrphid flies and *M. mellinum* between control and drift-treatment were observed.

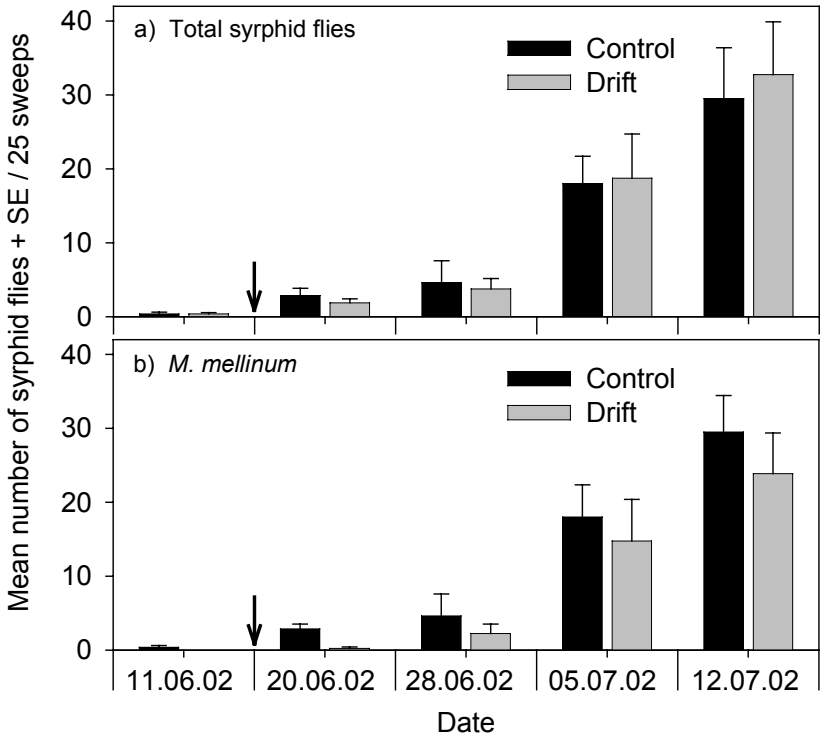

Fig. 9. Mean numbers (+ SE) of total **syrphid flies** (a) and ***M. mellinum*** (b) captured per 25 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2002. The arrow indicates date of insecticide application.

Count data 2003

In 2003 just cereal aphids were counted in sufficient numbers on wheat tillers to allow statistical analysis. Analysis of cereal aphid data was done at functional group level as well as at species level for the three species *R. padi*, *S. avenae*, and *M. dirhodum*. Mummified aphids and stages of chrysopids and syrphids first occurred in higher numbers (> 1 stage/50 tillers) at the third post-treatment count (7 July). Numbers of coccinellid adults and larvae found on wheat tillers in field margins remained low (< 1 stage/50 tillers) throughout the monitoring period.

Lambda-cyhalothrin drift into field margin strips significantly reduced total **cereal aphid** population densities at 1 m from the field edge compared to the control (t-test: df = 14, t = -2.80, p = 0.014) (Fig. 10a). This trend was also observed for ***R. padi*** *and* ***M. dirhodum***, though the decrease in population densities was not significantly different from the control (t-test (*R. padi*): df = 14, t = -1.87, p = 0.083; Satterthwaite t-test (*M. dirhodum*): df = 12.5, t = -1.89, p = 0.082) (Fig. 10b & c). Although the increase in mean population densities of ***S. avenae*** at 1 m was 7.8 fold higher in control strips than in drift strips, population dynamics did not differ significantly among each other (Satterthwaite t-test: df = 7.2, t = -1.26, p = 0.248) (Fig. 10d).

When compared with the control, no significant drift effects on cereal aphid populations, neither at functional group nor at species level, were detected at 2 m distance from the field edge.

Drift effects on aphids were transitory. Later counts did not reveal significant differences in population dynamics of total cereal aphids between control and drift-treatment at 1 or 2 m distance from the field edge. In control plots, a peak in cereal aphid densities was observed in mid July (Fig. 10a), followed by a sharp decline in numbers on 21 July. Contrarily, no clear peak in cereal aphid densities was recorded in drift plots (Fig. 10a).

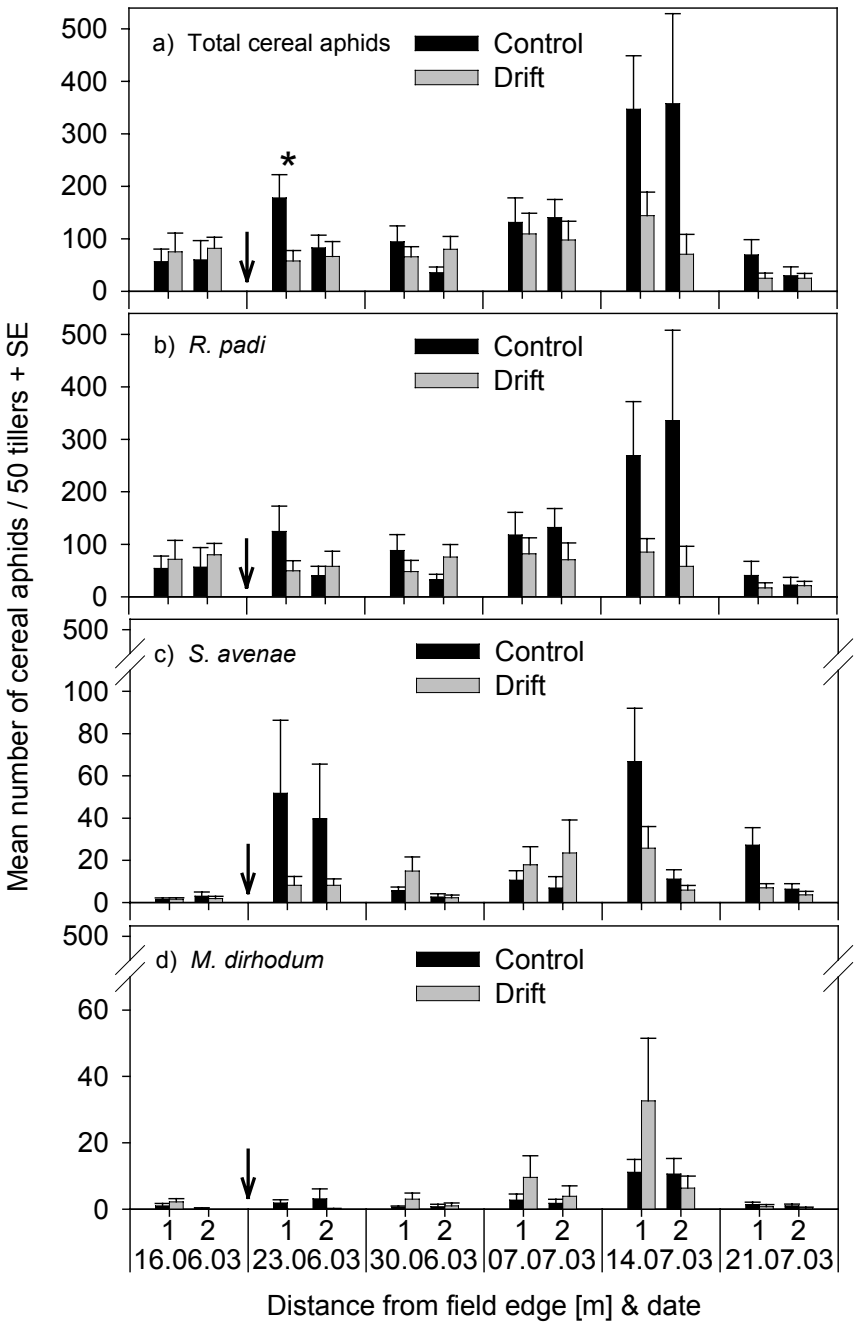

Fig. 10. Mean numbers (+ SE) of total **cereal aphids** (a), ***R. padi*** (b), ***S. avenae*** (c), and ***M. dirhodum*** (d) per 50 tillers within the field margin strips at 1 and 2 m distance from the field edge before and after the application of λ-cyhalothrin to wheat fields in 2003. Asterisks indicate statistically significant differences ($p < 0.05$) in population changes between control and drift-treatment. The arrow indicates date of insecticide application.
Result t-test (total cereal aphids, 23.06.03, 1 m): df = 14, t = -2.80, p = 0.014.

Sweep net data 2003

In 2003, apterous and alate aphids, total coccinellids (adults and larvae pooled), chrysopid larvae, and syrphid flies were captured in sufficient numbers to allow statistical analysis. In addition, analysis at species level was possible for the syrphid species *E. balteatus*, *E. corollae*, and *S. scripta*.

Low numbers of mummified aphids observed during the first four counts in 2003 (cf. Fig. 6a) already indicated that aphid parasitoids occurred late in the season; they were captured in higher numbers (> 1 specimen per 50 sweeps) in the last two samplings.

Lambda-cyhalothrin drift into field margin strips seemed to have an adverse effect on **apterous aphid** population densities. Although densities decreased in both control (-156 ± 43 SE aphids/50 sweeps) and drift field margin strips (-330 ± 77 SE aphids/50 sweeps), the decrease was higher, though insignificantly (t-test: $df = 14$, $t = -1.97$, $p = 0.069$), in field margins contaminated by insecticide drift (Fig. 11a). This tendentious difference in population dynamics between control and drift field margin strips was transitory and not observed on any subsequent sampling date. Population densities of apterous aphids peaked in mid July, followed by a decline in densities on 23 July (Fig. 11a).

As apterous aphids, numbers of **alate aphids** decreased following the insecticide application in both control and insecticide drift-contaminated field margin strips (Fig. 11b). Overall, population dynamics of alate aphids did not differ significantly between control and drift plots. Winged aphids peaked in mid July both in control and drift plots, followed by a drop in numbers on 23 July (Fig. 11b).

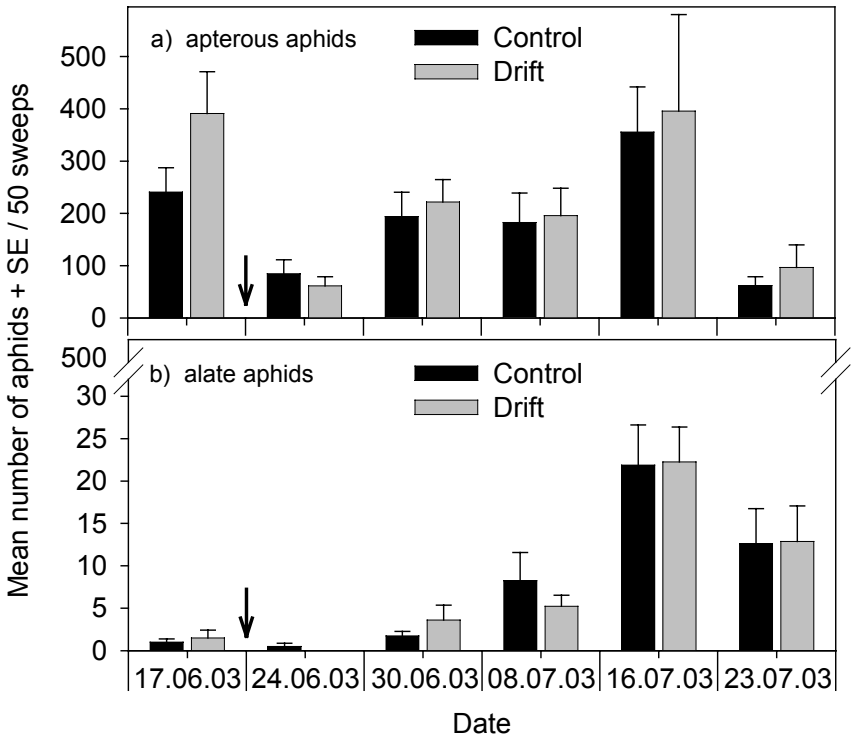

Fig. 11. Mean numbers (+ SE) of **apterous** (a) and **alate** (b) **aphids** per 50 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2003. The arrow indicates date of insecticide application.

The first post-treatment sweep sample revealed a decrease in **coccinellid** densities in both control and drift field margin strips compared to pre-treatment samples (Fig. 12). The population decline in coccinellids was significantly higher in λ-cyhalothrin drift-contaminated field margins than in control margins (t-test: df = 14, t = -2.41, p = 0.030). A significant difference in the population dynamics of coccinellids between drift and control treatment was again detected on 8 July (Satterthwaite t-test: df = 8.9, t = -2.41, p = 0.040) (Fig. 12). From 16 July coccinellid abundances increased in both control and drift field margin plots. On 23 July, almost one month subsequent to the insecticide application, coccinellid densities in drift field margins nearly recovered to pre-treatment densities; at the same time, densities in the control exceeded pre-treatment levels (Fig. 12).

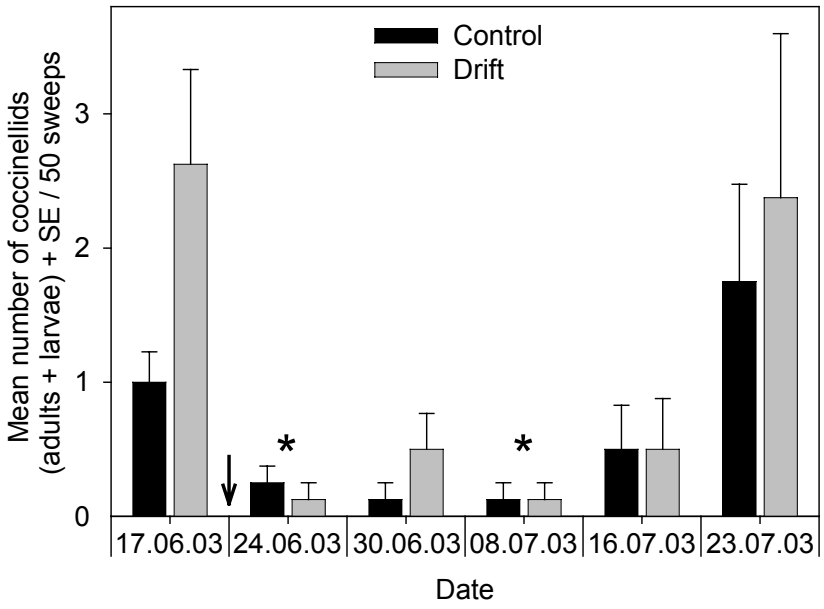

Fig. 12. Mean numbers (+ SE) of **coccinellids** captured per 50 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2003. Asterisks indicate statistically significant differences ($p < 0.05$) in population changes between control and drift-treatment. The arrow indicates date of insecticide application. Results t-test (24.06.03): df = 14, t = -2.41, p = 0.030; Satterthwaite t-test (08.07.03): df = 8.9, t = -2.41, p = 0.040.

Compared to pre-treatment catches, numbers of **chrysopid larvae** decreased subsequent to the insecticide application in both control and drift plots (Fig. 13). But abundances increased over time and exceeded the pre-treatment levels on 8 July. Overall, no significant differences in population dynamics of chrysopid larvae between control and insecticide drift-contaminated field margin strips were detected.

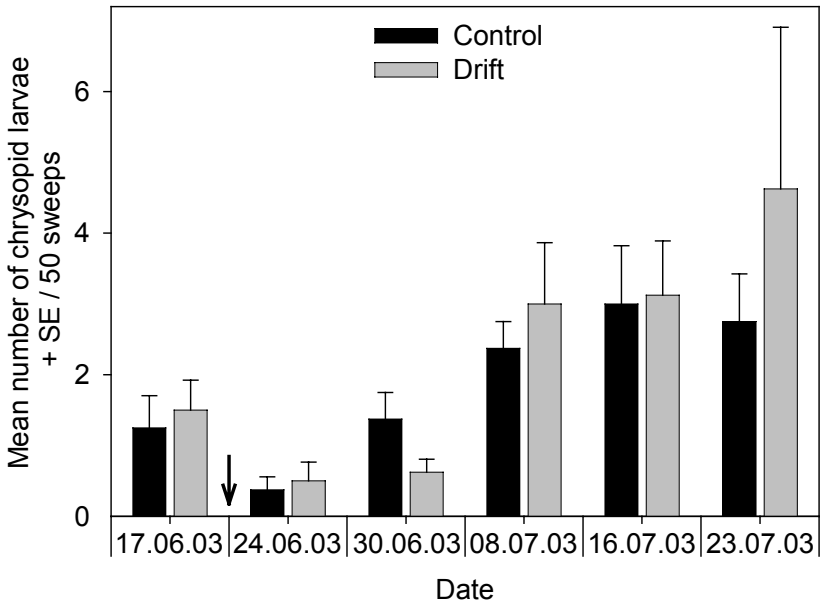

Fig. 13. Mean numbers (+ SE) of **chrysopid larvae** per 50 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2003. The arrow indicates date of insecticide application.

Pre-treatment catches of **syrphid flies** were very low, with a mean of 1.4 and 2.1 syrphids per 50 sweeps in control and drift field margins, respectively. *S. scripta* comprised nearly 80 % of total pre-treatment catches. The first post-treatment sample on 24 June revealed that densities of total syrphids, *E. corollae*, and *E. balteatus* sharply increased in both control and insecticide drift-contaminated field margin strips, whereas densities of *S. scripta* slightly decreased (Fig. 14a to d). Neither at functional group nor at species level was the population development of syrphids in the control significantly different from that in the drift-treatment.

Numbers of ***E. corollae*** gradually declined from 30 June (Fig. 14b). A similar trend, interrupted by a slight increase on 8 July, was observed in the population dynamics of ***E. balteatus*** (Fig. 14c). On 17 and 23 July catches of both species, *E. corollae* and *E. balteatus*, were very low (mean ≤ 1.1 specimen/50 sweeps). Overall, no significant differences between control and drift plots were observed.

Subsequent to the application, the population development of ***S. scripta*** was contrary to that observed for *E. corollae* and E*. balteatus*. Numbers increased from 30 June and levelled off to a mean of about two to three specimens per 50 sweeps from 8 July to 23 July (Fig. 14d). There were no significant differences in catches of *S. scripta* between control and drift field margin strips on any sampling date.

The only indication that the population dynamics of syrphids in the control were different from that in the drift field margins was given by the statistical analysis of total

syrphid fly catches. On 8 July, the population increase of syrphids in the control was almost significantly higher compared to that in the drift treatment (t-test: df = 14, t = -2.11, p = 0.053).

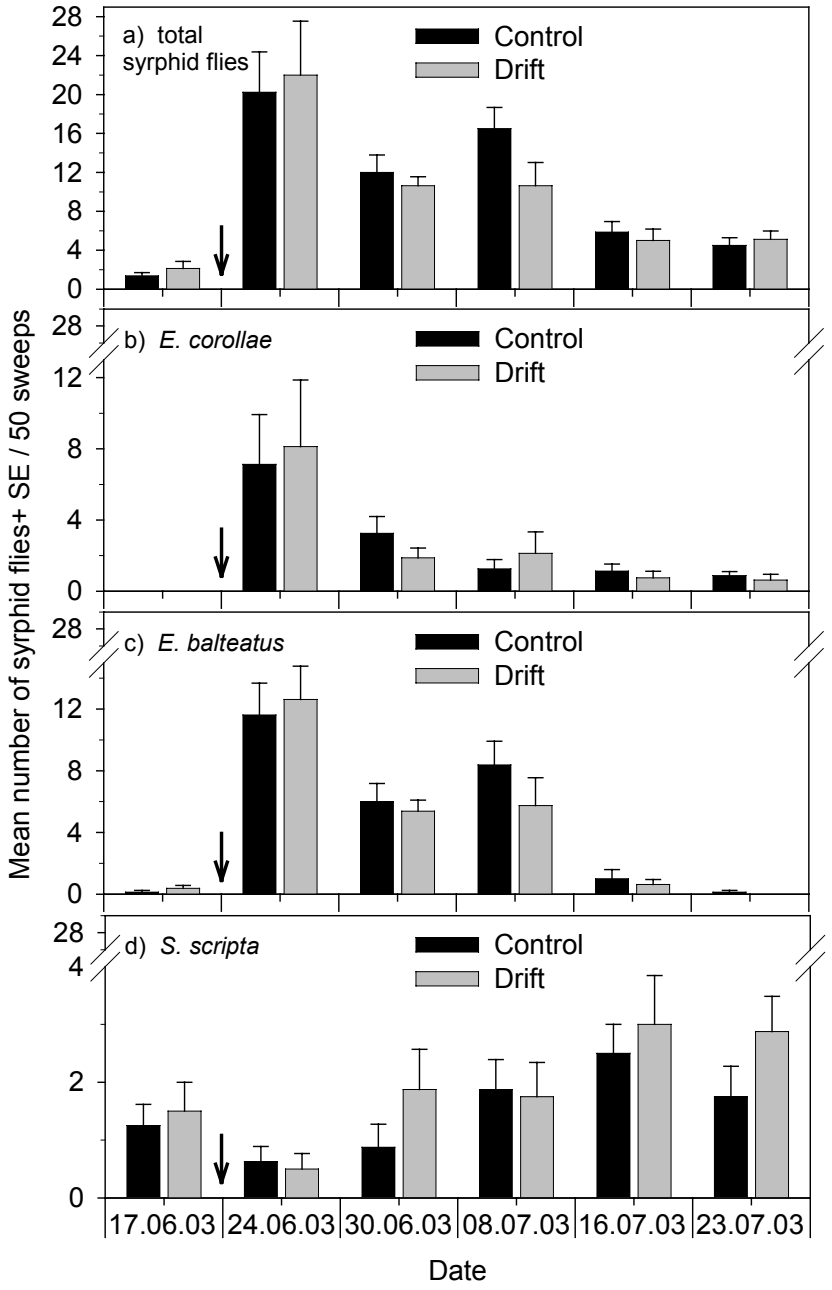

Fig. 14. Mean numbers (+ SE) of total **syrphid flies** (a), ***E. corollae*** (b), ***E. balteatus*** (c), and ***S. scripta*** (d) captured per 50 sweeps within the field margin strips before and after the application of λ-cyhalothrin to wheat fields in 2003. The arrow indicates date of insecticide application.

3.3.6 Influence of drift-contaminated and drift-protected field margins on within-crop population recovery through immigration

In the following section the terms “control” and “control (field) plot” refer to drift-protected control field margin strips and the adjacent wheat areas. The terms “drift” and “drift (field) plot” are used for insecticide drift-contaminated field margin strips and the areas within the wheat bordering on drift field margins (cf. Fig. 1, page 39).

Count data 2002

Data derived from visual counts in 2002 allowed statistical analysis of post-treatment population development at functional group level for cereal aphids, mummified aphids, and syrphid eggs. While counting, it was not possible to identify the species of hoverfly eggs found on the wheat tillers. However, it was supposed that the majority of eggs had been deposited by the two most frequently captured species, *M. mellinum* and *E. balteatus*. Larval stages of both *E. balteatus* and *M. mellinum* are aphidophagous. However, the latter also consume other insects (e.g. Dziock, 2002). Several studies have documented a positive aphid density-dependent oviposition response by female *E. balteatus* (e.g. Bargen et al., 1998; Sutherland et al., 2001b). Therefore, statistical analysis of syrphid egg “recovery” was performed with inclusion of aphid densities as covariate. However, it has to be kept in mind that *M. mellinum* may lay its eggs independent of aphid densities (Dziock, 2002).
In addition to analysis at functional group level, analysis at species level was performed for the three cereal aphid species *R. padi*, *M. dirhodum*, and *S. avenae*.

Compared to pre-treatment densities, the application of λ-cyhalothrin caused a decrease in numbers of **cereal aphids** at 25 m from the field edge in both wheat areas adjacent to control and drift field margin strips. Mean numbers of cereal aphids were significantly higher in the field margins than at 5 and 25 m into the wheat in both treatments (Fig. 15a). However, contrary to the drift treatment, higher numbers of cereal aphids were observed on 19 June in the control at 5 m from the field edge compared to pre-treatment densities. Furthermore, control densities at 5 m were significantly higher than at 25 m into the wheat, whereas drift densities at 5 and 25 m did not differ from each other (Fig. 15a). This difference between control and drift treatment was transitory. From 26 June until the end of the monitoring period, no significant differences among distances in control and drift treatment, respectively, were observed (Fig. 15a). Cereal aphids did not recover to pre-treatment densities.

The first post-treatment count on 19 June revealed an increase (19.3 ± 17.3 SE *R. padi*/50 tillers) in mean numbers of ***R. padi*** at 5 m into wheat areas next to control field margin strips compared to pre-treatment densities, whereas numbers adjacent to drift margins levelled off (Fig. 15b). At 25 m into the wheat pre- and post-treatment densities of *R. padi* were similar in both control and drift plots. Statistical analysis showed no significant differences in numbers of *R. padi* between distances, neither in control nor in drift plots. However, densities were nearly significantly higher in drift-protected control field margin strips than at 25 m from the field edge ($p = 0.018$). One week later, on 26 June, densities of *R. padi* declined at all distances, both in control and drift treatment. Numbers of *R. padi* were significantly higher in the field margins than at 5 and 25 m into the field, but within-field densities did not differ significantly from each other (Fig. 15b). From 9 July, no significant differences in *R. padi* densities between distances were detected in control plots, whereas on 9 July numbers in drift plots were significantly lower at 25 m than at 5 m into the wheat and in the field margin. Additionally, numbers of *R. padi* were significantly higher in field margins than at 5 and 25 m from the field edge on 23 July (Fig. 15b).

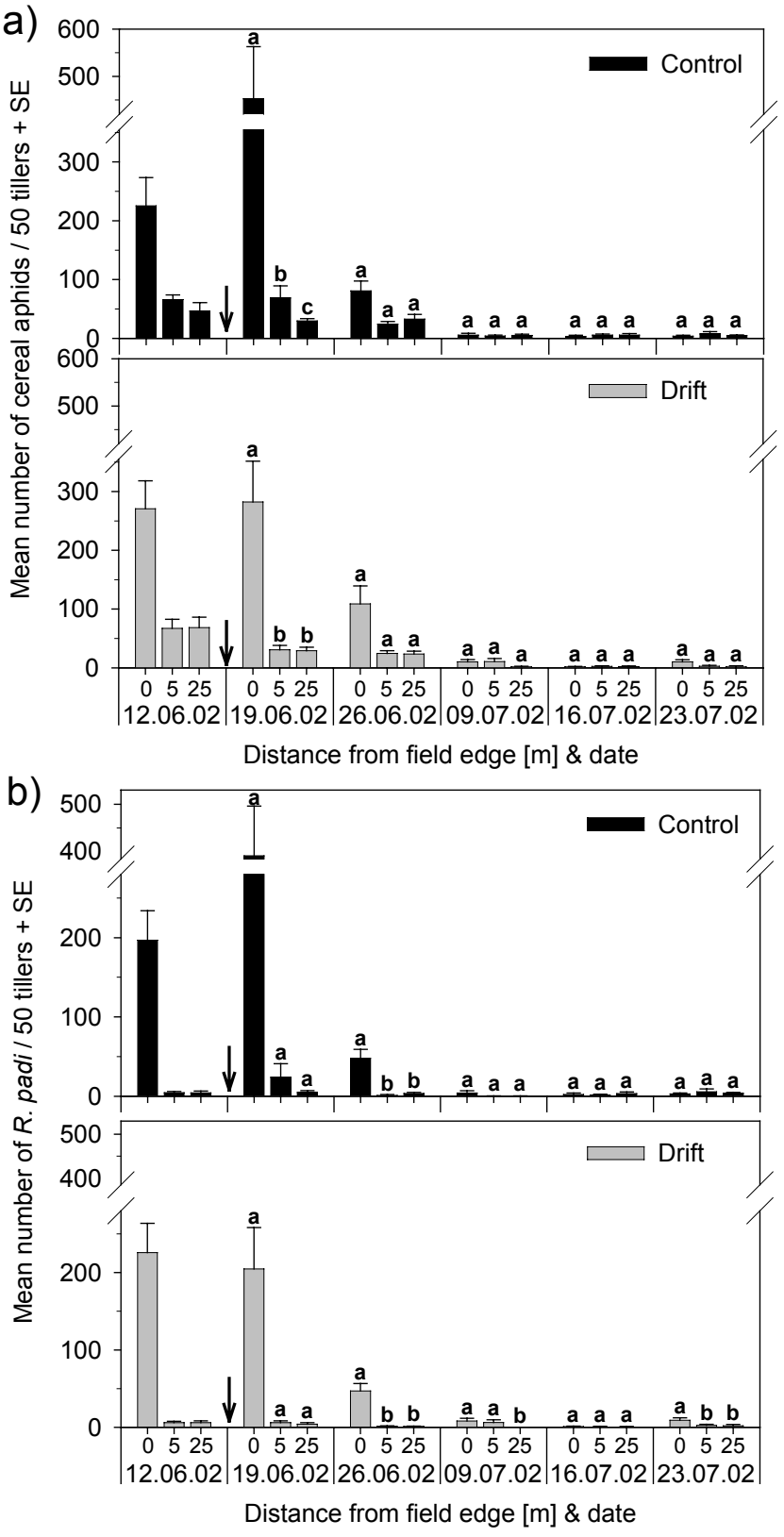

Fig. 15. Population development of **cereal aphids** (a) and ***R. padi*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Subsequent to the application of λ-cyhalothrin to wheat fields, numbers of ***M. dirhodum*** at 5 and 25 m into the wheat declined in both control and drift plots, whereas in field margin strips densities increased (Fig. 16a). From 9 July population densities of *M. dirhodum* sharply declined at all distances and did not recover to pre-treatment densities. Overall, numbers of *M. dirhodum* did not differ significantly between distances, neither in control nor in drift plots (Fig. 16a).

Abundances of ***S. avenae*** decreased following the insecticide application both at 5 and 25 m from the field edge in control and drift plots compared to pre-treatment densities. On 19 June no significant differences were detected between distances in the control, whereas in the drift treatment numbers were significantly higher in field margins than at 25 m from the field edge (Fig. 16b). On June 26 significantly higher population abundances were observed in field margins than at 5 and 25 m in both control and drift plots (Fig. 16b). This difference was transitory, on 9 July a sharp decrease in densities of *S. avenae* in drift and control field margins was observed. Thus, as for *M. dirhodum* and total cereal aphids, statistical analysis did not show any significant difference in numbers of *S. avenae* among distances from 9 to 23 July.

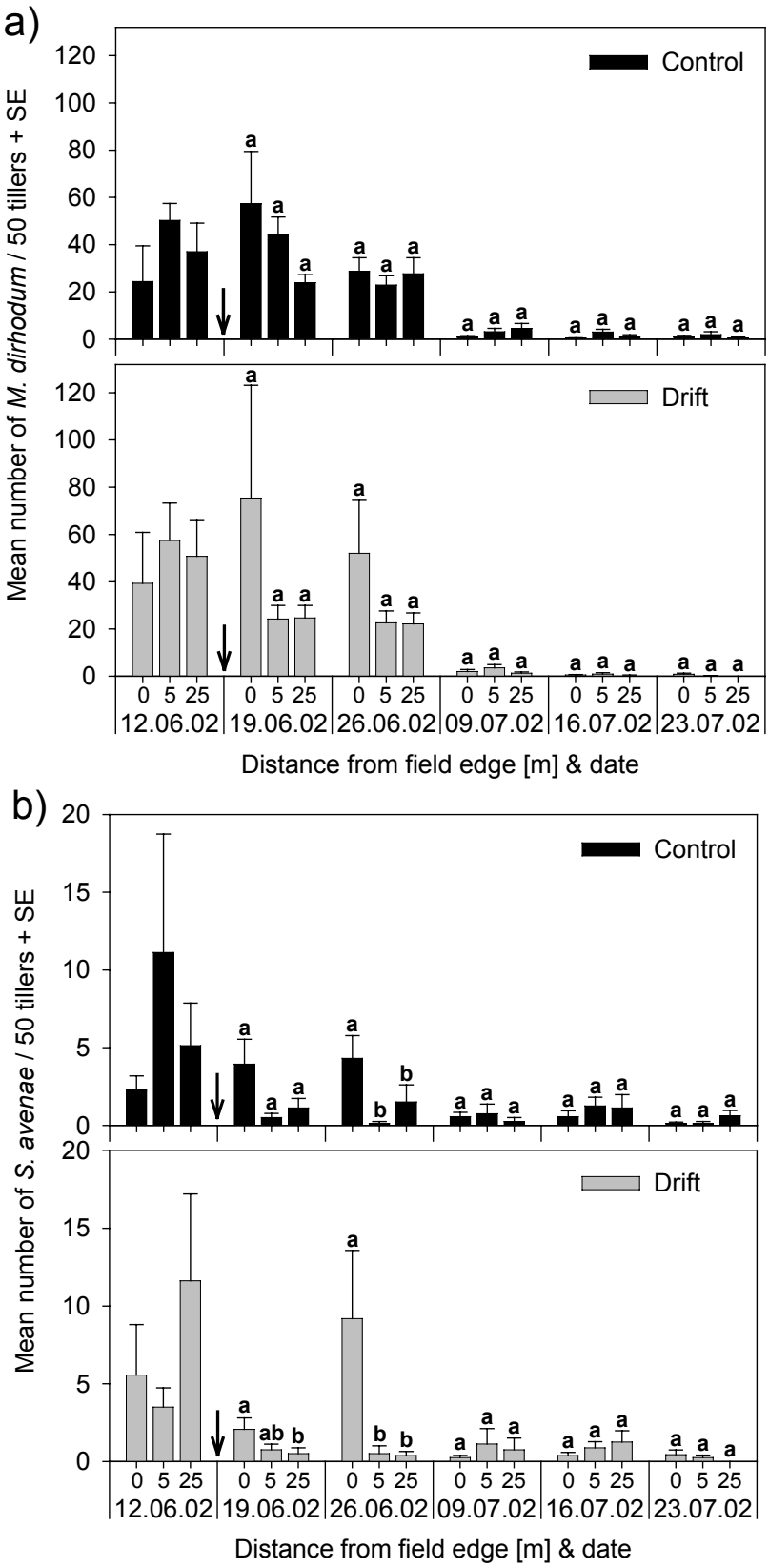

Fig. 16. Population development of ***M. dirhodum*** (a) and **S*. avenae*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

The first post-treatment count revealed an increase in **mummy** densities compared to pre-treatment densities at all distances from the field edge both in control and drift plots (Fig. 17). In the control significantly more mummified aphids were detected at 5 m than at 25 m, whereas in the drift plots similar mummy densities were found at any distance. From 26 June to 23 July similar trends in the population development of mummies were observed in control and drift plots. On 26 June mummy densities in the field margins were significantly higher than densities at 5 and 25 m into the wheat (Fig. 17). Subsequently, numbers of mummies decreased at all distances and no significant differences in densities among distances were found from 9 to 23 July.

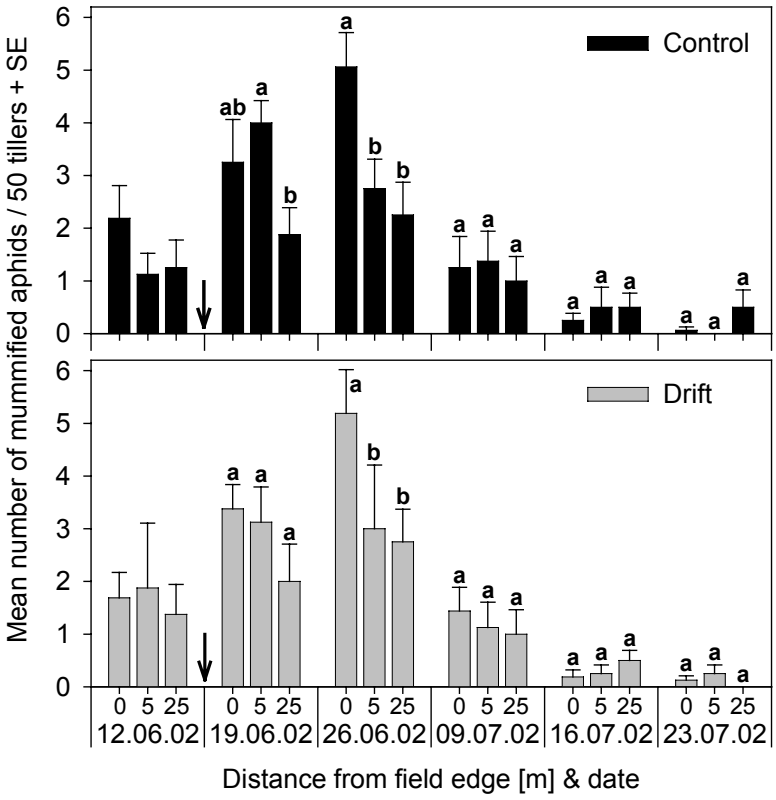

Fig. 17. Population development of **mummified aphids** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

The first post-treatment count on 19 June revealed an increase in densities of **syrphid eggs** at almost all distances in control and drift plots, respectively (Fig. 18). Most eggs were found in field margins, where aphid densities were highest (cf. Fig. 15a). On 26 June a decrease in numbers of syrphid eggs was observed in control field margin strips and adjacent wheat areas at 5 m from the field edge, whereas numbers at 25 m slightly increased. At the same time numbers levelled off in drift plots. From 9 July syrphid egg densities declined at most distances in both control and drift plots (Fig. 18), as did aphid densities (cf. Fig. 15a). However, relatively high numbers of syrphid eggs (mean from 2.3 to 2.5 eggs/50 tillers) were detected in control plots at 5 and 25 m on 16 July and at 5 m on 23 July. These were laid independently of aphid densities on wheat tillers (cf. results ATS, Tab. A4, appendix). Overall, there were no significant differences in numbers of syrphid eggs among distances in control and drift plots, respectively (Fig. 18).

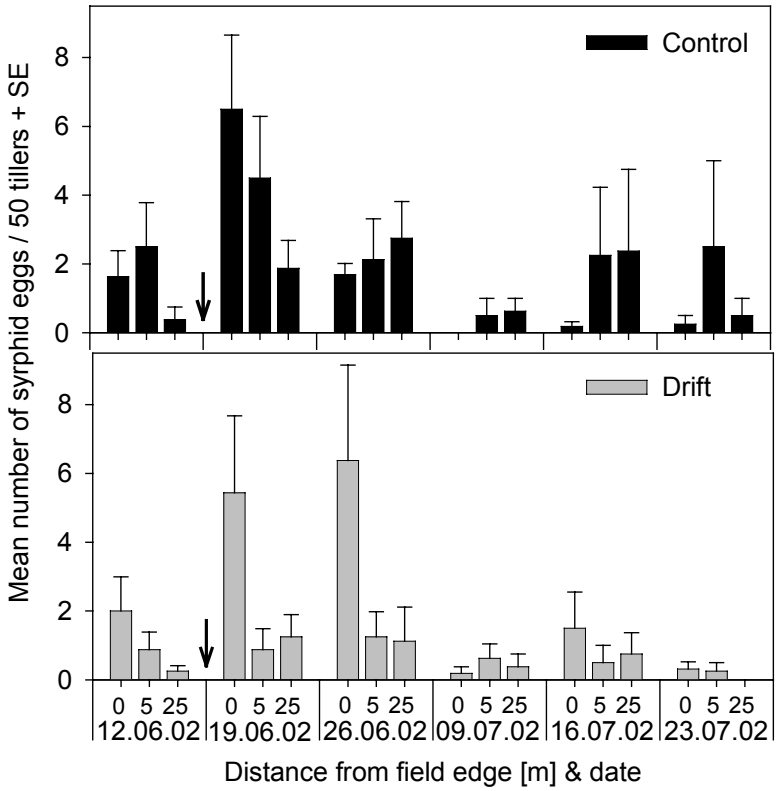

Fig. 18. Population development of **syrphid eggs** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Statistical analysis did not reveal significant differences in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Sweep net data 2002

Data derived from sweep netting in 2002 allowed statistical analysis of post-treatment population dynamics at functional group level for apterous and alate aphids, cereal aphid parasitoids, adult syrphids, and chrysopid larvae. Additionally, analysis at the species level was performed for the syrphid species *M. mellinum* and *E. balteatus* and for the cereal aphid parasitoid species *A. uzbekistanicus*-group and *A. picipes*.

Subsequent to the application of λ-cyhalothrin to wheat fields, densities of **apterous aphids** in both control and drift treatment decreased at 4 and 24 m from the field edge compared to pre-treatment densities, whereas numbers in field margins increased (Fig. 19a). The first post-treatment sweep sample revealed significantly higher densities of apterous aphids in drift field margins than at 4 and 24 m into the wheat, whereas in the control no significant difference was detected among numbers captured in the field margin and at 4 m from the field edge. Significantly fewer wingless aphids were captured at 24 m than at 4 m and in the margin (Fig. 19a). The same trend was observed on 28 June in the control, whereas there were no significant differences in apterous aphid densities between distances in the drift treatment. On 5 July significantly lower numbers of apterous aphids were captured at 4 and 24 m from the field edge compared to the field margins of both control and drift treatment. Finally, on 12 July no significant differences in densities of wingless aphids were detected among distances (Fig. 19a).

Following the application population densities of **alate aphids** increased at all distances compared to pre-treatment densities. On 20 June significantly higher numbers of winged aphids were captured in field margins compared to wheat areas at 4 and 24 m from the field edge in both control and drift plots (Fig. 19b). Numbers captured at 4 and 24 m were similar. On 28 June a decrease in numbers of alate aphids was observed at all distances. No significant differences were detected between densities in field margins and densities within the field in both control and drift treatment. Similar numbers of wingless aphids were captured at all distances in the last two sweep samplings in control and drift plots, respectively. Numbers were low (mean ≤ 2.5 alate aphids/25 sweeps).

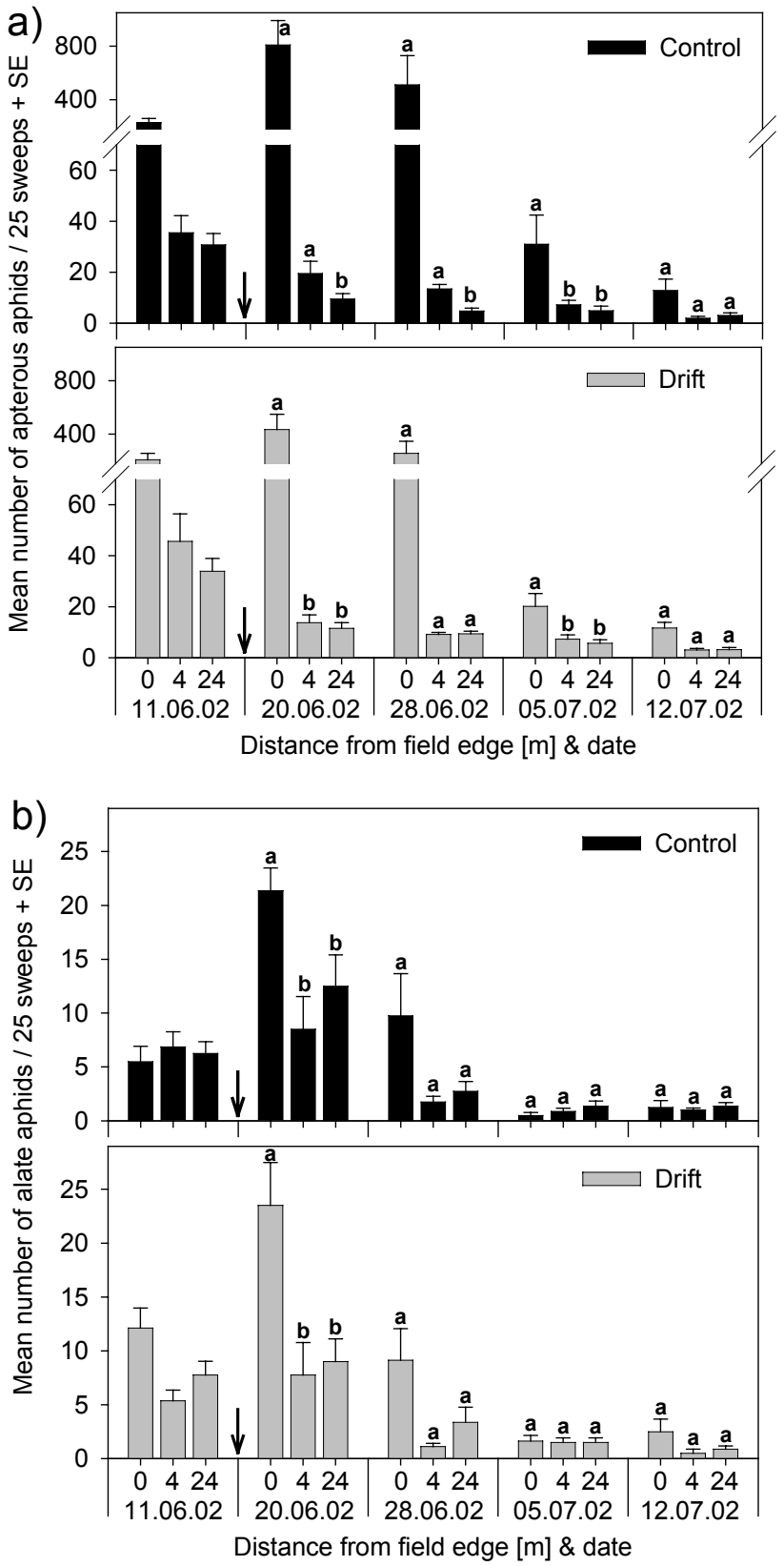

Fig. 19. Population development of **apterous** (a) and **alate** (b) **aphids** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

More **cereal aphid parasitoids** were captured on the first post-treatment sampling date compared to pre-treatment catches at all distances both in control and drift plots (Fig. 20). Statistical testing revealed no significant differences in densities among distances. On 28 June low numbers of cereal aphid parasitoids (mean < 1.2 per sweep sample) were captured by sweep netting. As pointed out above (cf. drift effects on parasitoids), this weak capture efficacy was related to the relatively strong wind (mean 4.5 m/s) while sweep netting was performed (cf. 5.3.3). In subsequent samplings higher numbers of cereal aphid parasitoids were collected at all distances in both control and drift plots. Overall, there were no significant differences in densities of total cereal aphid parasitoids between distances on any sampling date (Fig. 20).

For a more detailed interpretation of the post-treatment population development of cereal aphid parasitoids, analysis was also conducted at species level for the two most abundant species, *A. uzbekistanicus*-group and *A. picipes* (see below).

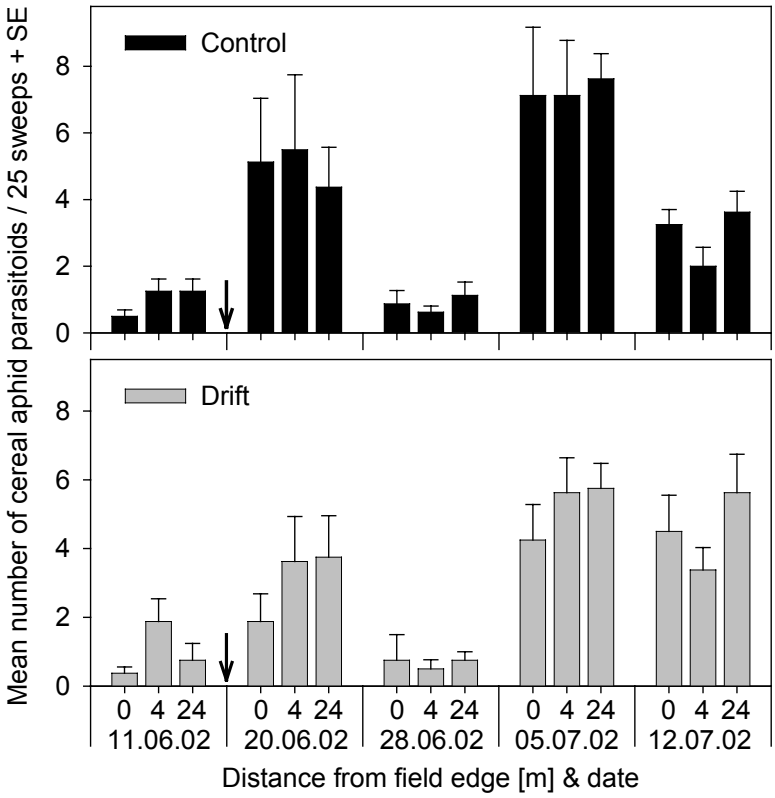

Fig. 20. Population development of **cereal aphid parasitoids** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Statistical analysis did not reveal significant differences in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

On the whole, trends observed in the post-treatment population dynamics of the ***A. uzbekistanicus*-group** were similar to those observed in total cereal aphid parasitoids. Except for a significantly lower number of specimens of the *A. uzbekistanicus*-group captured in control plots at 4 m compared to 24 m and the field margin on 12 July, no significant differences were detected in parasitoid densities among distances on any sampling date (Fig. 21a).

On 11 June few ***A. picipes*** were captured within-field (mean ≤ 1 specimen/25 sweeps) but none in the field margin strips of control and drift plots, respectively. Subsequent to the application, on 20 June, *A. picipes* were present in the field margins of both control and drift plots (Fig. 21b). Parasitoid numbers at different distances from the field edge did not differ significantly from each other. On 28 June a slight decrease in numbers of *A. picipes* collected by sweep netting was recorded (reasons for the low capture are given above). On 5 and 12 July densities of *A. picipes* tended to be higher at 4 and 24 m than within the field margin strips of control and drift treatment, respectively. However, just on 5 July significantly more parasitoids were captured at 24 m from the field edge than in the field margin strips of control plots (Fig. 21b).

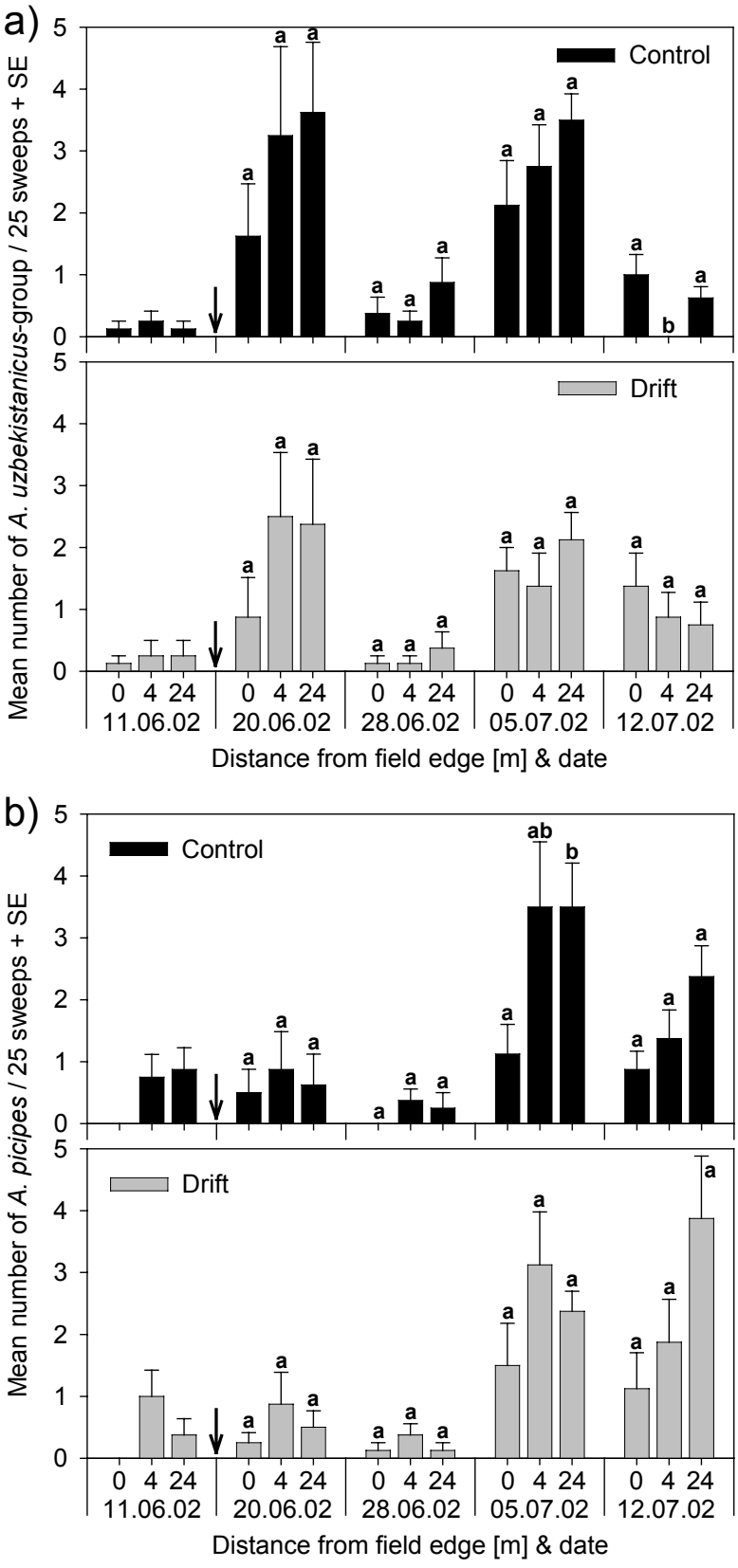

Fig. 21. Population development of the ***A. uzbekistanicus*-group** (a) and ***A. picipes*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Pre-treatment densities of **syrphid flies** were low (mean ≤ 0.5 syrphids/25 sweeps) at all distances from the field edge in control and drift plots, respectively. Subsequent to the insecticide application, numbers of syrphids captured per 25 sweeps within field margins increased gradually from a mean of 3 (control) and 2 (drift), respectively, on 20 June to a mean of 30 (control) and 33 (drift), respectively, on 12 July (Fig. 22). Within-field densities of syrphids remained low throughout the sampling period (mean < 6 syrphids/25 sweeps) in both, control and drift plots (Fig. 22). On 29 June numbers of hoverflies in control field margin strips were significantly higher than those at 4 and 24 m from the field edge, whereas in drift plots numbers within field margins and at 4 m did not differ from each other, but both differed significantly from numbers captured at 24 m. On 28 June similar trends in the population dynamics of syrphid flies were observed in control and drift plots. Population densities of syrphids within field margins were significantly higher than those at 24 m from the field edge, but were equal to those at 4 m. Furthermore, densities at 4 and 24 m did not differ significantly from each other. One week later significantly more syrphids were captured within field margins compared to wheat areas at 4 and 24 m from the field edge in both control and drift plots. Similar differences in population densities among distances were recorded in control plots on 12 July, whereas in drift plots densities significantly decreased with distance from the field edge (Fig. 22).

For a more detailed interpretation of the post-treatment population development of syrphid flies analysis was also conducted at species level for the two most abundant species, *M. mellinum* and *E. balteatus* (see below).

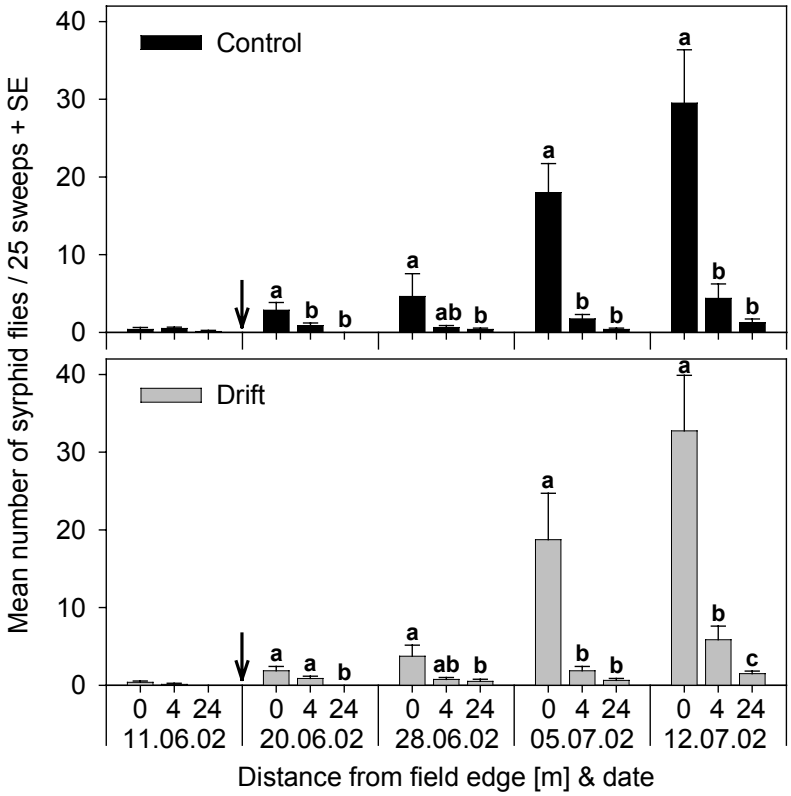

Fig. 22. Population development of **syrphid flies** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

The population development of the most frequently captured species ***M. mellinum*** was similar to that previously described for total syrphid flies. However, the first two post-treatment catches revealed no significant differences in densities of *M. mellinum* among distances in control and drift plots, respectively (Fig. 23a). On 5 and 12 July numbers of *M. mellinum* were significantly higher in control field margins than in wheat areas at 4 and 24 m from the field edge, whereas in drift plots numbers significantly decreased with distance into the wheat (Fig. 23a).

Overall, population dynamics of ***E. balteatus*** did not differ greatly between control and drift treatment. On 20 June significantly more *E. balteatus* were captured in control field margin strips than at 24 m from the field edge, whereas in drift plots no significant differences were detected. One week later there were no significant differences in numbers of *E. balteatus* between distances in control and drift plots (Fig. 23b). On 5 and 12 July numbers of *E. balteatus* increased in both control and drift field margins; densities were significantly higher than those at 4 and 24 m into the wheat.

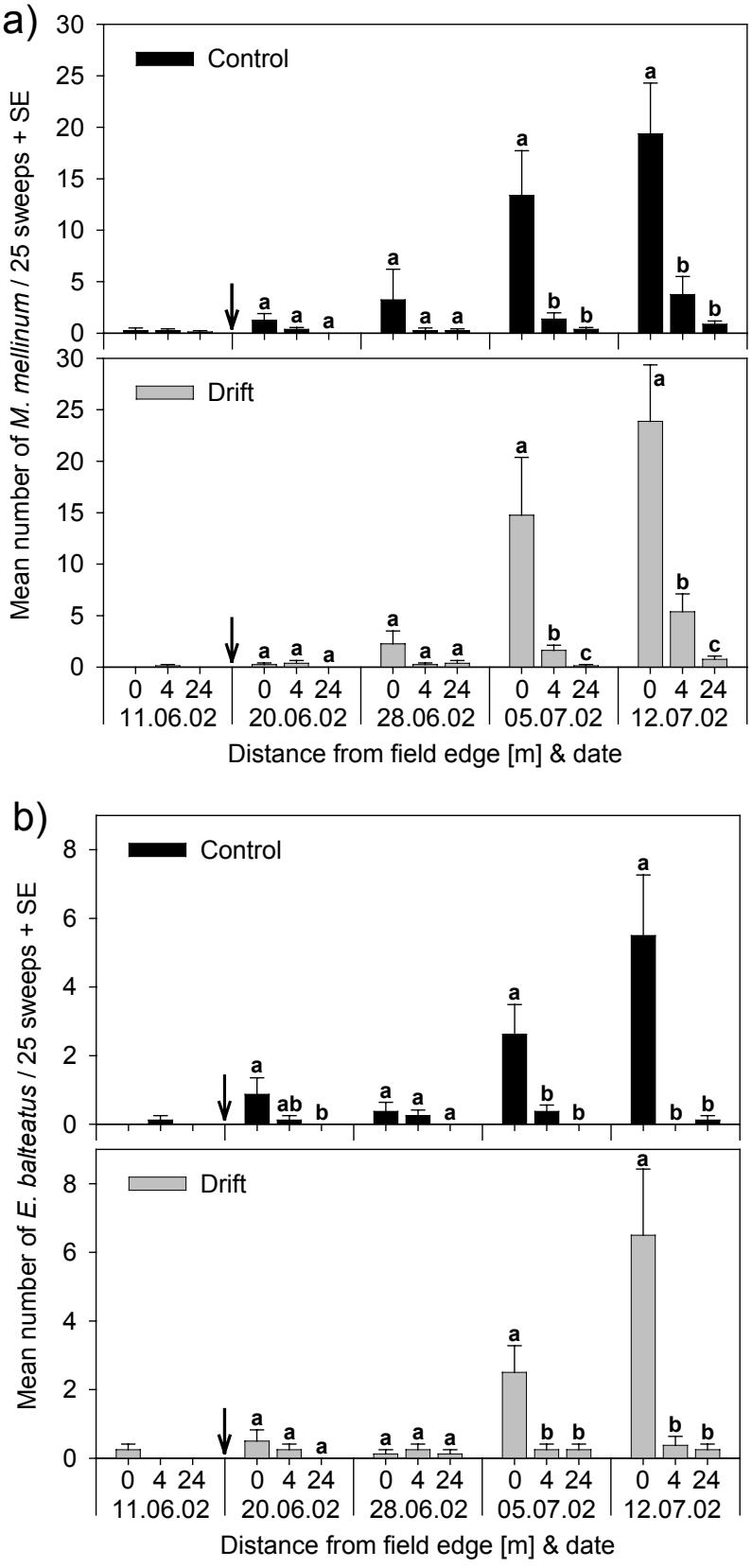

Fig. 23. Population development of ***M. mellinum*** (a) and ***E. balteatus*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Throughout the sampling period **chrysopid larvae** were captured in low numbers (mean < 1.4 larvae/25 sweeps) in control and drift plots, respectively (Fig. 24). Overall, population densities of chrysopid larvae in field margins and in wheat areas at 4 and 24 m from the field edge did not differ significantly from each other both in control and drift plots.

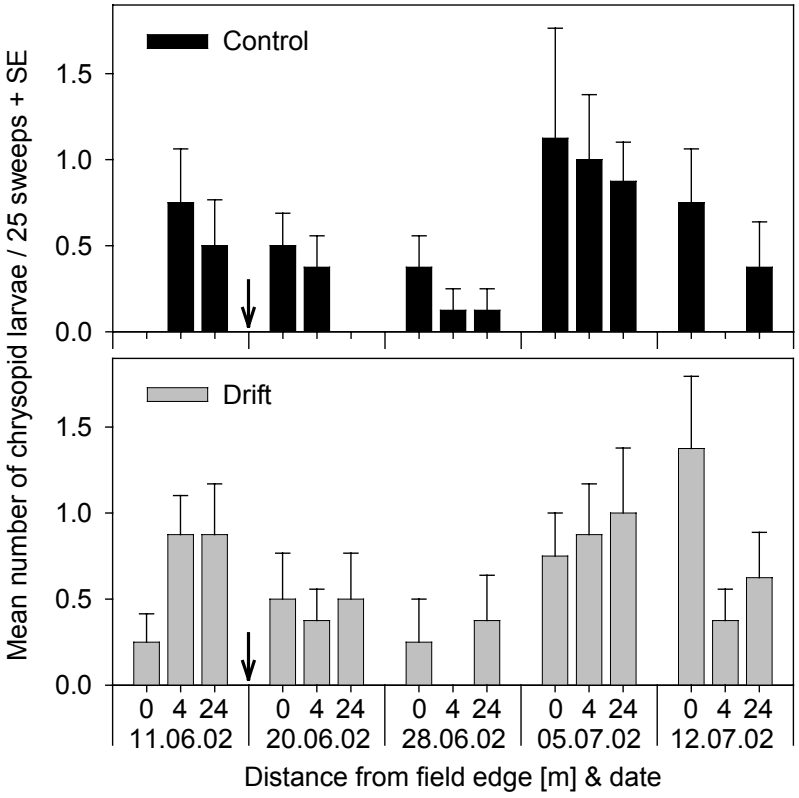

Fig. 24. Population development of **chrysopid larvae** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Statistical testing did not reveal significant differences in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Count data 2003

Data derived from visual counts in 2003 allowed statistical analysis of post-treatment population development at functional group level for cereal aphids and chrysopid eggs. In addition, analysis at species level was performed for the three cereal aphid species *R. padi, M. dirhodum*, and *S. avenae*.

Subsequent to the application of λ-cyhalothrin to wheat fields, numbers of **cereal aphids** in control field margin strips increased compared to pre-treatment densities. A significant increase in population densities with distance into the wheat was detected (Fig. 25a), i.e. significantly more cereal aphids were found in wheat areas at 5 m than at 24 m. Contrarily, post-spray cereal aphid densities in drift field margins on 23 June were slightly lower than pre-treatment densities. In spite of that, numbers were significantly higher than those at 4 and 24 m from the field edge (Fig. 25a). The latter did not differ significantly from each other. From 30 June to 21 July no significant differences in cereal aphid population densities between distances were detected in control plots (Fig. 25a). In drift field margins aphid numbers were significantly higher than at 24 m into the wheat on 30 June. But from 7 to 21 July there were no significant differences in numbers of cereal aphids between distances in drift plots (Fig. 25a). On 7 July cereal aphid population densities increased at all distances in control and drift plots, respectively. Aphids peaked in mid July and then declined.

Analysis at species level indicated similar population dynamics of ***R. padi*** both in control and drift plots (Fig. 25b). On the first three post-treatment monitoring dates (i.e. 23 June to 7 July) densities of *R. padi* were significantly higher in field margins than in wheat areas at 5 and 25 m from the field edge (Fig. 25b). Owing to an increase in within-field densities on 14 July, no significant differences in numbers of *R. padi* among distances were detected. Additionally, on the last date of monitoring population densities of *R. padi* did not differ significantly amongst distances in control and drift plots, respectively.

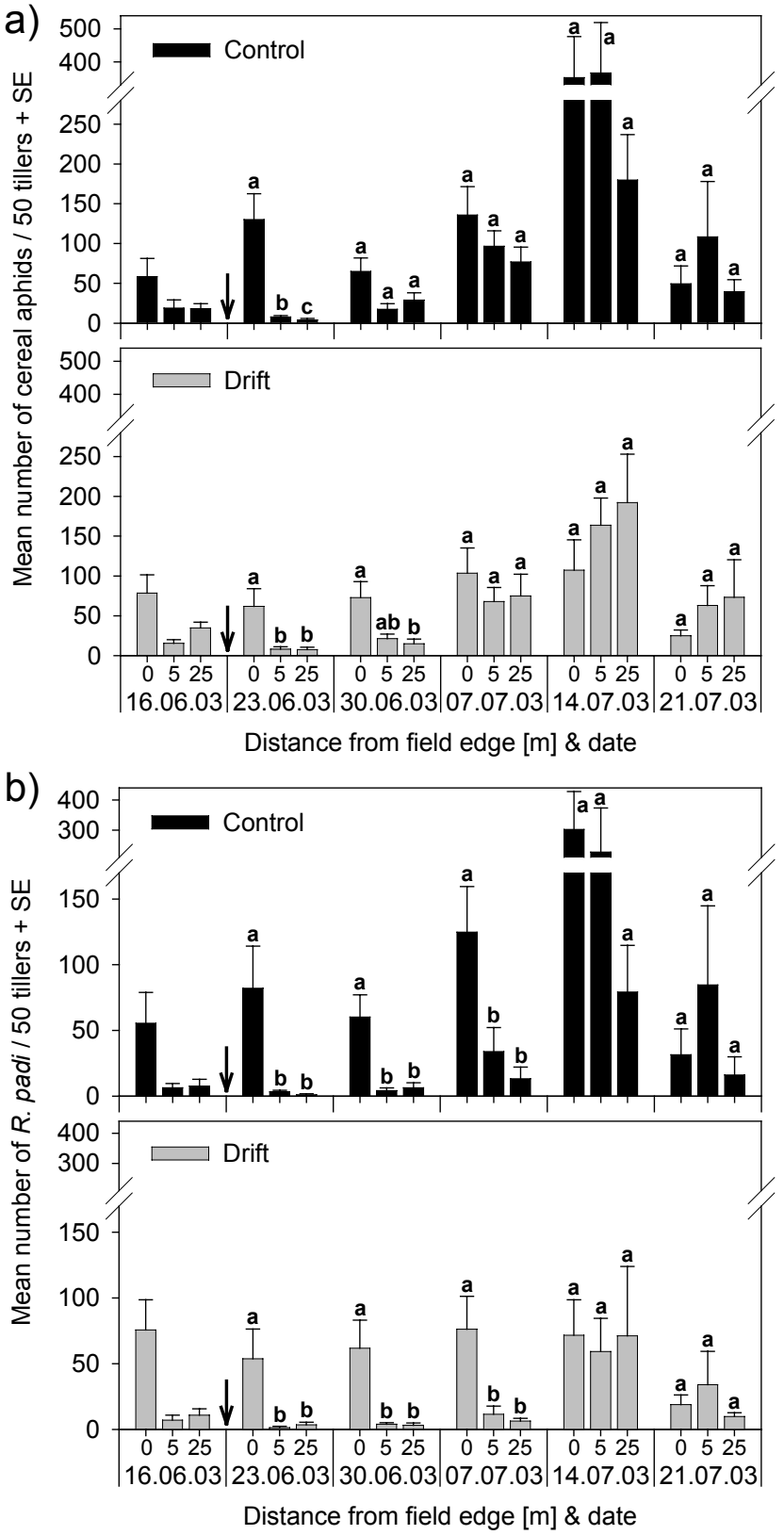

Fig. 25. Population development of total **cereal aphids** (a) and ***R. padi*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Pre-treatment population densities of ***M. dirhodum*** were low at all distances (mean 0.3 to 7.6 *M. dirhodum*/50 tillers) both in control and drift plots (Fig. 26a), as were initial post-treatment densities (mean ≤ 2.5 *M. dirhodum*/50 tillers). There were no significant differences in numbers of *M. dirhodum* amongst distances. From 30 June to 14 July within-field population densities increased gradually, resulting in significantly higher numbers of *M. dirhodum* at 5 and 25 m than in the field margins of both control and drift plots (Fig. 26a). On 21 July a sharp decline in numbers of this species was observed in control and drift plots, respectively. There were no significant differences in densities between distances.

On 23 June subsequent to the application of λ-cyhalothrin a sharp increase in numbers of ***S. avenae*** was observed in control field margin strips, whereas numbers in treated wheat areas decreased. As a result, population densities of *S. avenae* were significantly higher in the control field margin than at 5 and 25 m into the wheat, but densities of *S. avenae* were similar at all drift plot densities (Fig. 26b). On 30 June a sharp decrease in numbers of *S. avenae* was observed in control field margins, nonetheless numbers in field margins were significantly higher than at 5 and 25 m. Significantly more *S. avenae* were also recorded in drift field margins compared to wheat areas at 5 and 25 m from the field edge. From 7 to 14 July densities of *S. avenae* increased at all distances. There were no significant differences in densities between distances, except for significantly more *S. avenae* on 7 July in control field margin strips compared with wheat areas at 5 m (Fig. 26b).

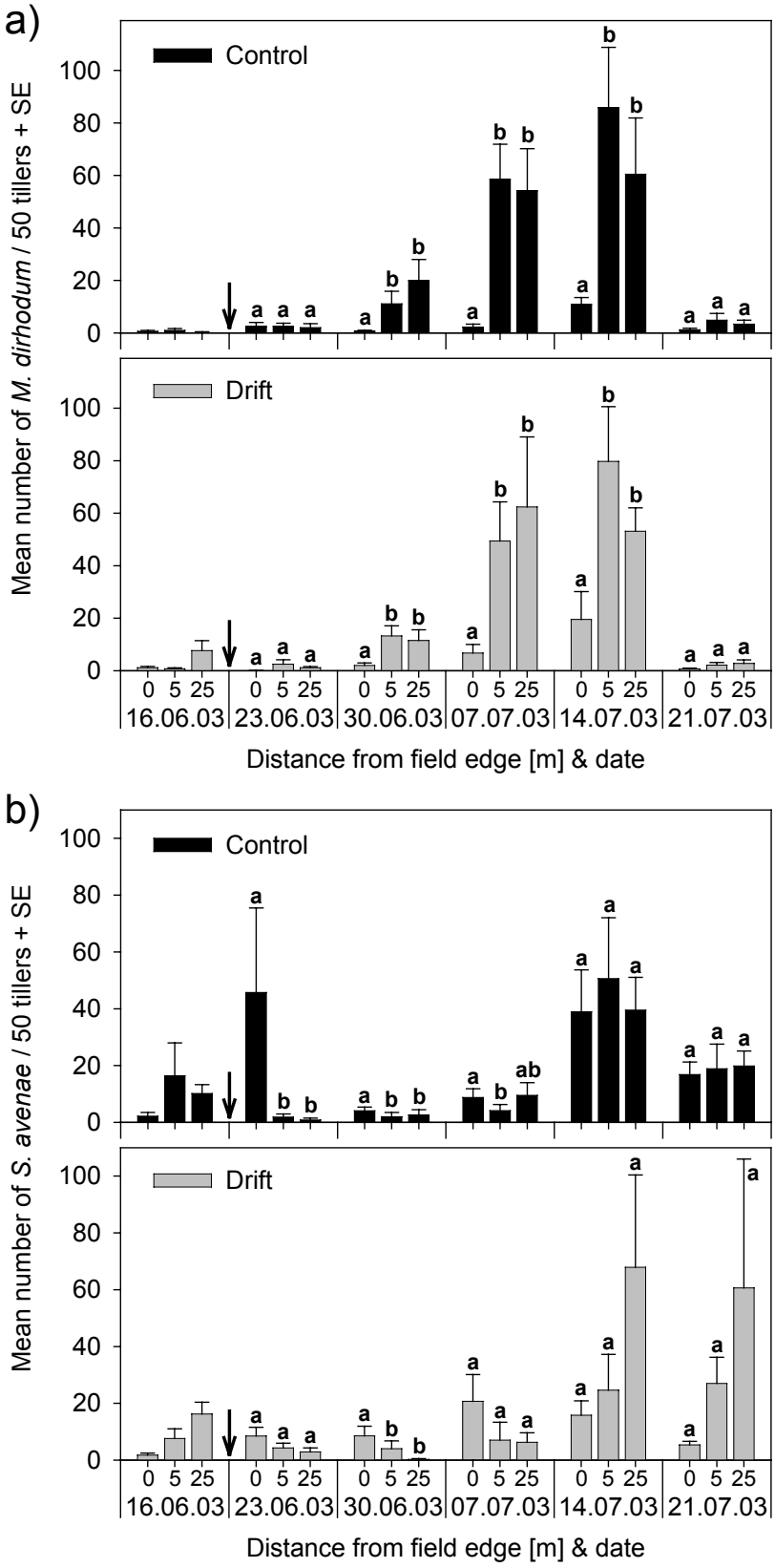

Fig. 26. Population development of ***M. dirhodum*** (a) and ***S. avenae*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

The first post-treatment count (23 June) revealed no significant differences in numbers of **chrysopid eggs** amongst distances in the control, whereas significantly lower densities of chrysopid eggs were observed in drift margins than in wheat areas at 5 and 25 m, respectively, from the field edge (Fig. 27). One week later no significant differences in lacewing egg densities were detected between distances in control and drift plots, respectively. On 7 and 14 July the distribution of chrysopid eggs was similar in control and drift plots, with almost always significantly higher densities at 5 and 25 m than in the field margin strips. On the last monitoring date an increase in lacewing eggs was observed at 25 m from the field edge both in control and drift plots. Chrysopid egg numbers at 25 m were significantly higher than those at 5 m in control and drift plots, respectively. In the drift field plots densities at 25 m were also significantly higher than those in the field margins (Fig. 27).

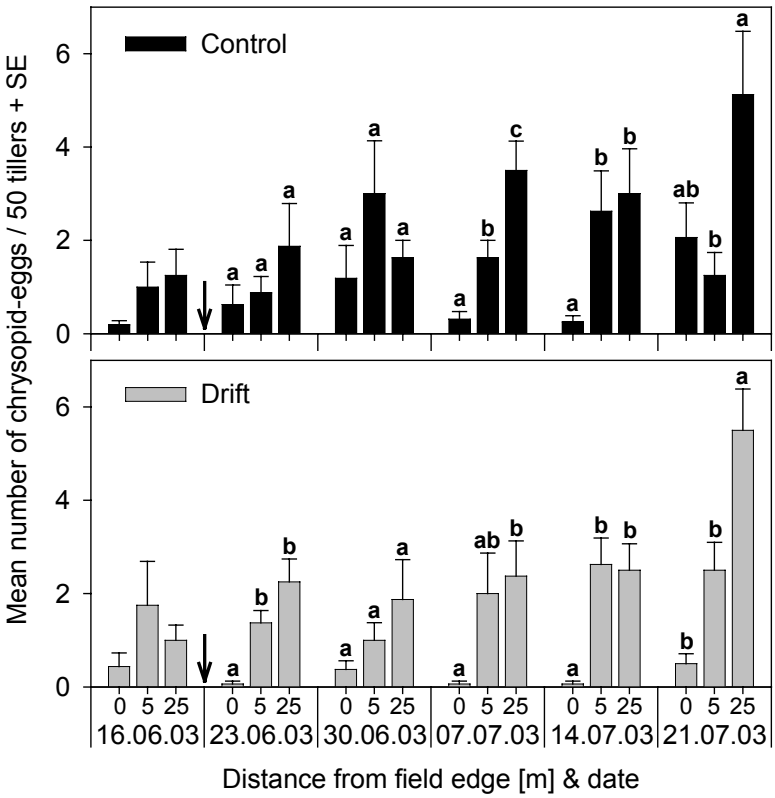

Fig. 27. Population development of **chrysopid eggs** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 5 and 25 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Sweep net data 2003

Data derived from sweep netting in 2003 allowed statistical analysis of post-treatment population development at functional group level for apterous and alate aphids, adult syrphids, adult *C. carnea*, chrysopid larvae, and aphidophagous coccinellids. Since adults and larvae of aphidophagous coccinellids belong to the same functional group, i.e. both prey on aphids, their numbers were pooled. Analyses at species level were performed for the syrphid species *E. balteatus*, *E. corollae*, *M. mellinum*, and *S. scripta* and for the cereal aphid parasitoid species-group *A. uzbekistanicus*-group.

Compared to pre-treatment densities numbers of **apterous aphids** initially decreased subsequent to the insecticide application at all distances both, in control and drift plots. As seen in 2002, the first post-treatment catch (24 June) revealed similar numbers of apterous aphids in control field margins and in adjacent (4 m) wheat areas, whereas in drift plots densities in field margins and at 4 m differed significantly from each other (Fig. 28a). Densities of wingless aphids were significantly lower at 24 m into the wheat than in the control and drift field margin strips, respectively. Similar differences amongst distances in both control and drift plots were detected on 30 June. From 30 June to 16 July populations of apterous aphids grew at all distances. From 8 July there were no significant differences in numbers of wingless aphids between distances in control plots. In drift plots this trend was first observed eight days later, on July 16.

As apterous aphids, **alate aphids** declined following the insecticide application at all distances in control and drift plots, respectively (Fig. 28b). On June 24 there were no significant differences in numbers of winged aphids among distances in drift plots, whereas in control field margins significantly more alate aphids were captured than at 24 m into the wheat. In both control and drift plots numbers of winged aphids gradually increased from 30 June to 16 July (Fig. 28b). From 30 June until the end of the sampling period no significant differences in population densities of alate aphids among distances were detected in control plots. However, on 16 July numbers of alate aphids seemed to increase with distance from the field edge. In drift plots on 8 and 16 July, respectively, significantly more winged aphids were captured at 4 and 24 m from the field edge than in the field margin. Finally, alate aphid densities declined at all distances on 23 July.

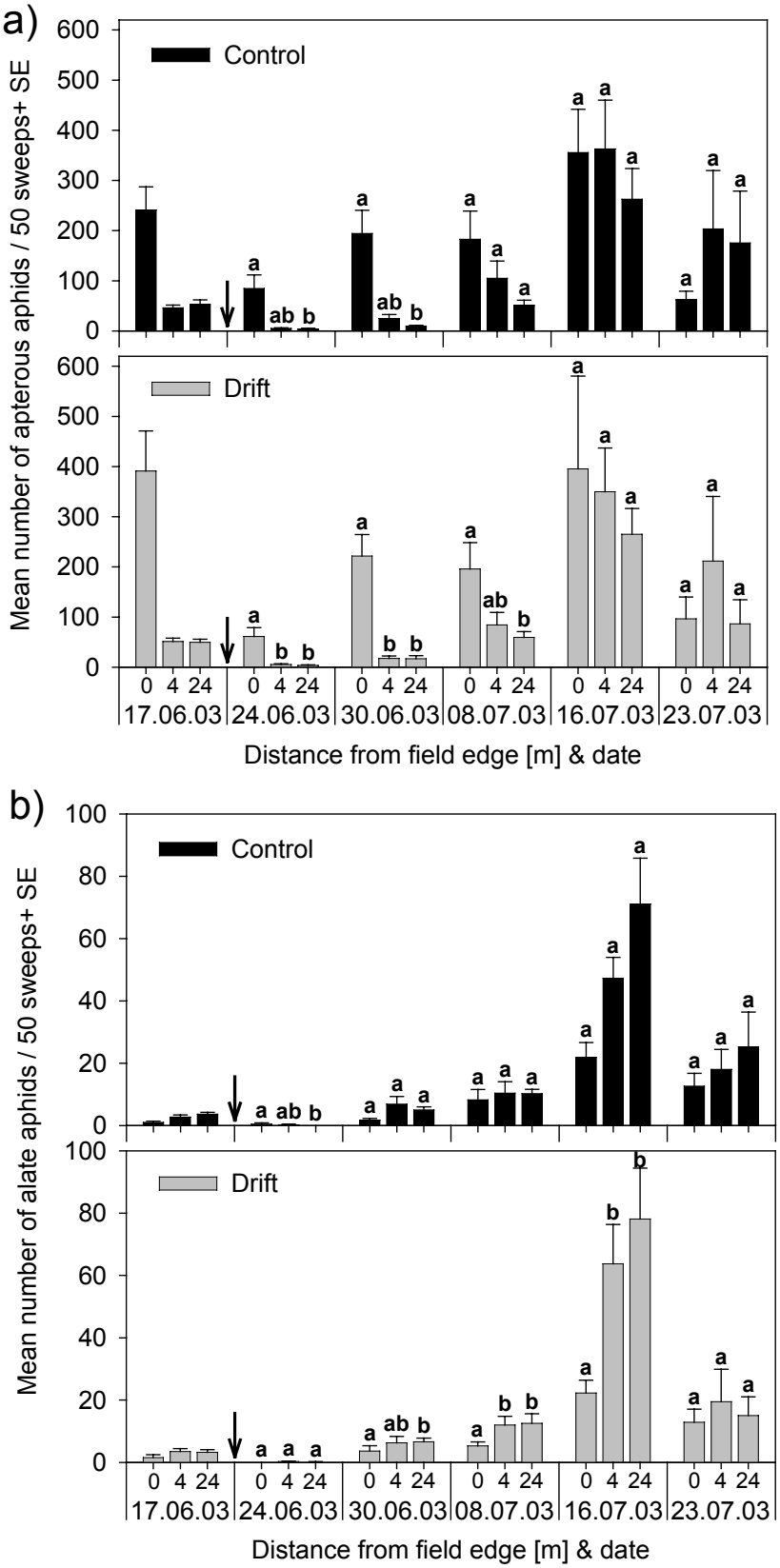

Fig. 28. Population development of **apterous** (a) and **alate** (b) **aphids** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Pre-treatment densities of adult syrphids were low (mean ≤ 2 syrphids/50 sweeps) at all distances in both control and drift plots (Fig. 29). On 24 June, following the insecticide treatment, numbers sharply increased in field margin strips to a mean of 20 and 22 syrphids/50 sweeps in control and drift plots, respectively. Significantly more hoverflies were captured in field margins than in wheat areas at 4 and 24 m from the field edge. Whereas in drift plots numbers were similar at 4 and 24 m, significantly more syrphids were caught in control plots at 4 than at 24 m (Fig. 29). In both control and drift field margins a decrease in numbers of syrphids was observed on 30 June. However, numbers were still significantly higher than in the wheat areas, where densities significantly decreased with distance from the field edge. From 8 to 23 July population densities of syrphids gradually decreased. At the end of the monitoring period population densities of aphidophagous hoverflies in field margins were significantly higher than those at 4 and 24 m in control and drift plots, respectively (Fig. 29).

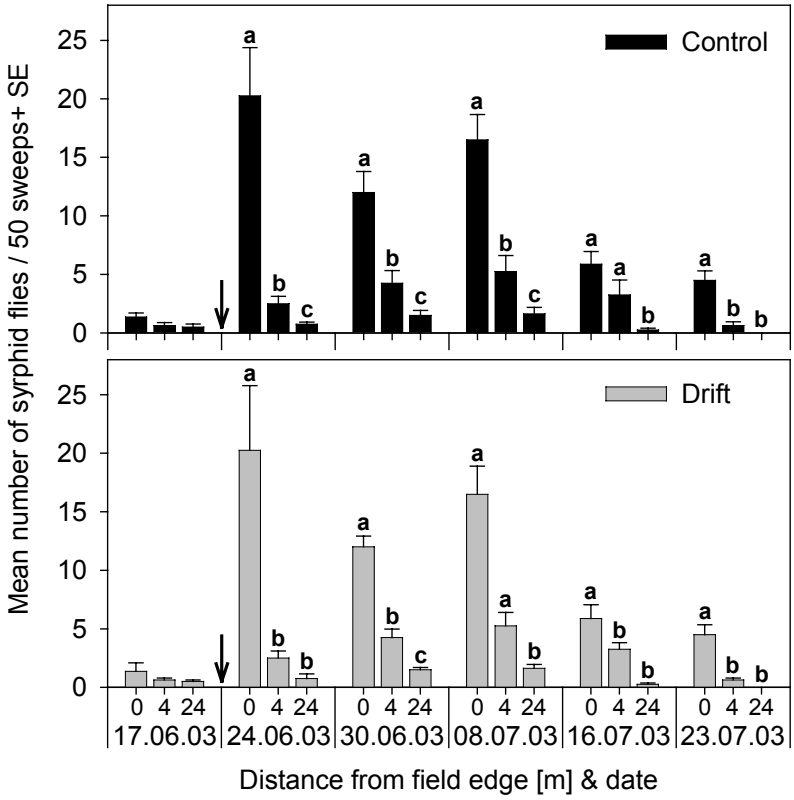

Fig. 29. Population development of **syrphid flies** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Subsequent to the insecticide application, numbers of ***E. balteatus*** sharply increased in field margin strips of control and drift plots, respectively (Fig. 30a). Significantly more hoverflies were captured in field margins than in wheat areas at 4 and 24 m from the field edge. Densities of *E. balteatus* at 4 and 24 m did not differ significantly from each other in both control and drift plots. Although fewer *E. balteatus* were captured in control and drift field margins, respectively, on June 30 compared to June 24, densities were significantly higher in field margins than at 4 and 24 m into the wheat. Within-field population densities significantly decreased with distance from the field edge (Fig. 30a). The spatial pattern of population densities of *E. balteatus* observed on 8 July did not differ greatly from that observed on 30 June. However, no significant difference between numbers of *E. balteatus* captured in control field margins and those collected at 4 m were detected. Sweep samplings on 16 and 23 July revealed a sharp decline in population densities of *E. balteatus* at all distances in both control and drift plots. There were no significant differences in densities amongst distances (Fig. 30a).

No ***E. corollae*** was captured prior to the insecticide treatment, neither in control nor in drift plots (Fig. 30b). On 24 June densities of *E. corollae* were significantly higher in control and drift plots, respectively, than in wheat areas at 4 and 24 m from the field edge. The latter did not differ significantly from each other. As seen for *E. balteatus*, fewer *E. corollae* were captured in control and drift field margins, respectively, on 30 compared to 24 June. Numbers were significantly higher in drift field margins than at 4 and 24 m, whereas numbers of *E. corollae* in control field margins were just significantly higher than numbers at 24 m, but similar to those at 4 m (Fig. 30b). From 8 to 23 July population densities of *E. corollae* declined in both control and drift plots. During that period *E. corollae* were not captured at each within-field distance, but they were always present, although in low numbers, in the field margin strips.

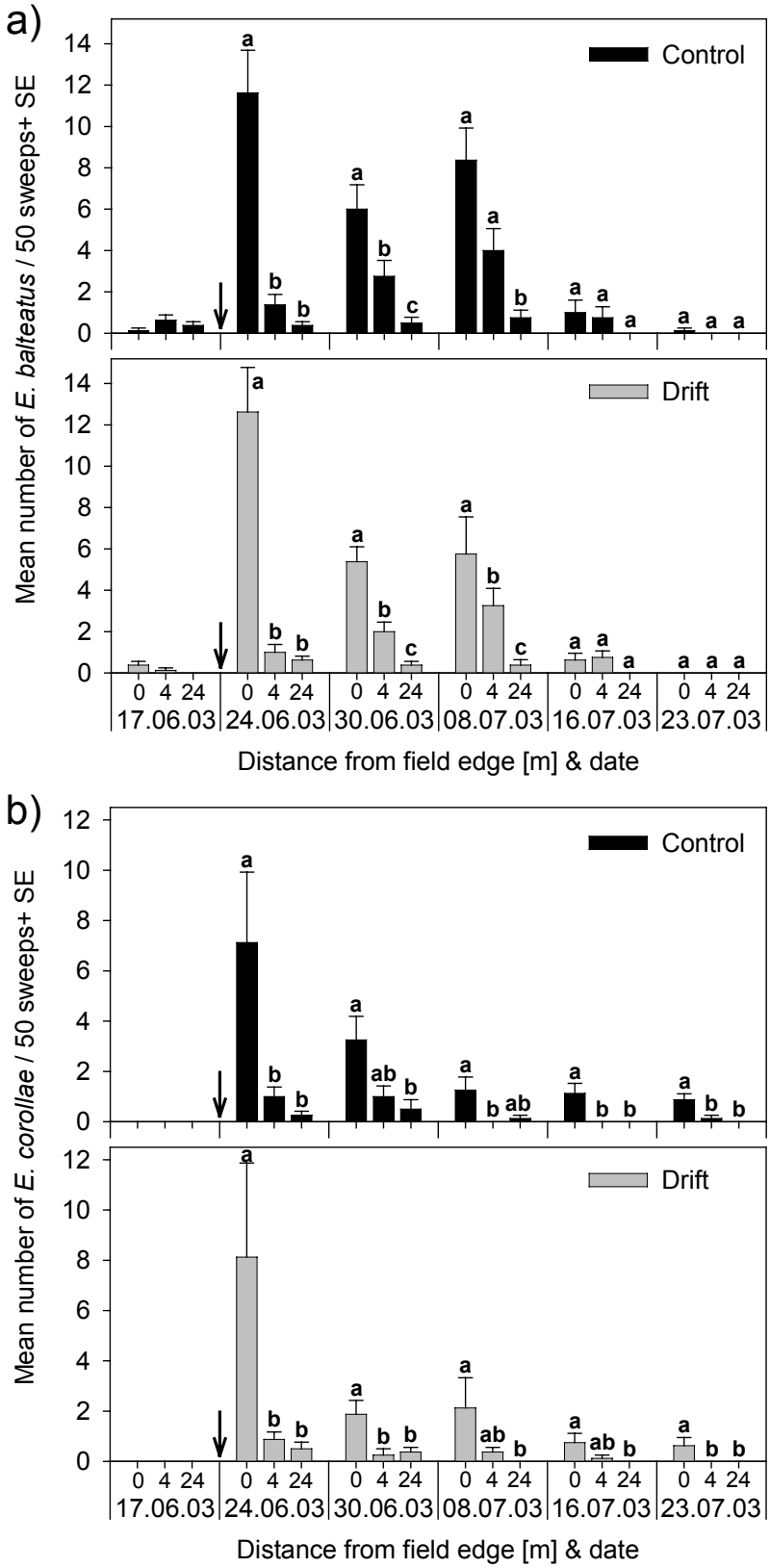

Fig. 30. Population development of ***E. balteatus*** (a) and ***E. corollae*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Pre-treatment densities of ***M. mellinum*** were very low (mean ≤ 0.3 specimens/50 sweeps). Whereas *M. mellinum* was captured at each drift plot-distance, it was only caught at 24 m in control plots (Fig. 31a). Following the application numbers increased in both control and drift field margin strips. On 24 June significantly more *M. mellinum* were captured in control field margins than in wheat areas at 4 and 24 m from the field edge, whereas similar densities were detected among drift plot distances. Compared to 24 June, numbers of *M. mellinum* increased at all distances in both control and drift plots on 30 June (Fig. 31a). Significantly more *M. mellinum* were captured in control field margin strips than at 4 and 24 m from the field edge, whereas in drift plots similar numbers were captured in field margins and at 4 m into the wheat; these were significantly higher than those at 24 m from the field edge. There were no significant differences in densities of *M. mellinum* among distances in control and drift plots, respectively, on 8 July. Again, there were no significant differences in numbers of *M. mellinum* among distances in drift plots on 16 July, whereas in control plots significantly more specimens were collected in the field margin and at 4 m, respectively, than at 24 m from the field edge. The last sweep sample on 23 July revealed a similar trend in the spatial population dynamics of *M. mellinum* in control and drift plots. Significantly more syrphids were captured in the field margins than within-field (Fig. 31a).

Throughout the whole period of sweep sampling ***S. scripta*** was predominantly captured in field margins of both control and drift plots (Fig. 31b). Except for two events where *S. scripta* was captured at 4 m from the field edge (on 24 June in control plots and on 8 July in drift plots, respectively), no specimens were captured within-field during the first three post-treatment sweep samplings (Fig. 31b). On 16 July, however, *S. scripta* was captured at each distance both in control and drift plots, with numbers being significantly higher in the field margins than at 4 and 24 m from the field edge. Finally, on 23 July significantly more *S. scripta* were captured in the field margins than at 4 and 24 m from the field edge in control and drift plots, respectively. No specimens were caught at 24 m into the wheat.

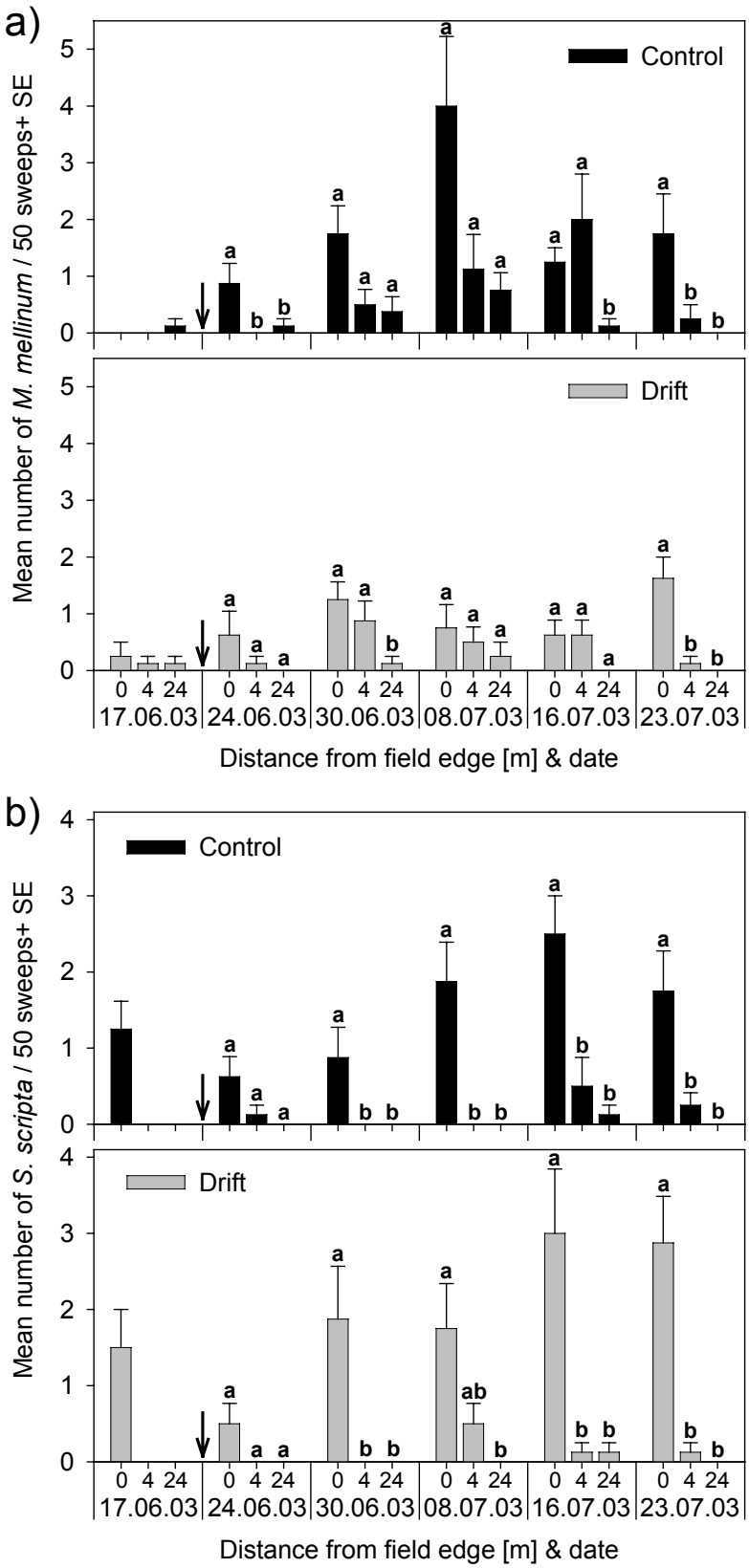

Fig. 31. Population development of ***M. mellinum*** (a) and ***S. scripta*** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

From 17 June to 8 July population densities of **cereal aphid parasitoids** were low (mean ≤ 1.3 paraitoids/50 sweeps) at all distances in both control and drift plots (Fig. 32a). There were no significant differences in parasitoid numbers among distances. On 16 July an increase in parasitoid population densities was observed at each distance in control and drift plots, respectively. In control plots similar numbers of parasitoids were captured per distance, whereas in drift plots significantly more parasitoids were captured at 24 m from the field edge than in the field margin strips. On 23 July a sharp increase in parasitoid densities was observed in control and drift plots, with no significant differences among distances (Fig. 32a). In drift plots numbers of parasitoids collected per 50 sweeps averaged to 10.8 (margin) and 10.3 (4 and 24 m, respectively) and in control plots to 11.8 (margin), 10.0 (4 m) and 13.3 (24 m).

Being the most frequently captured cereal aphid parasitoid species on the experimental sites, population dynamics of the ***A. uzbekistanicus*-group** were similar to those described above for total cereal aphid parasitoids. As previously mentioned, low numbers of parasitoids were captured on the first four sweep sampling dates. Specimens of the *A. uzbekistanicus*-group were constantly captured in wheat areas at 4 and 24 m from the field edge, but infrequently within field margin strips (Fig. 32b). On 16 and 23 July the spatial population development of the *A. uzbekistanicus*-group in control and drift plots, respectively, was similar to that described above for total cereal aphid parasitoids. Numbers of the *A. uzbekistanicus*-group were higher, though statistically insignificant, at 4 and 24 m from the field edge than in the control and drift field margin strips, respectively (Fig. 32b).

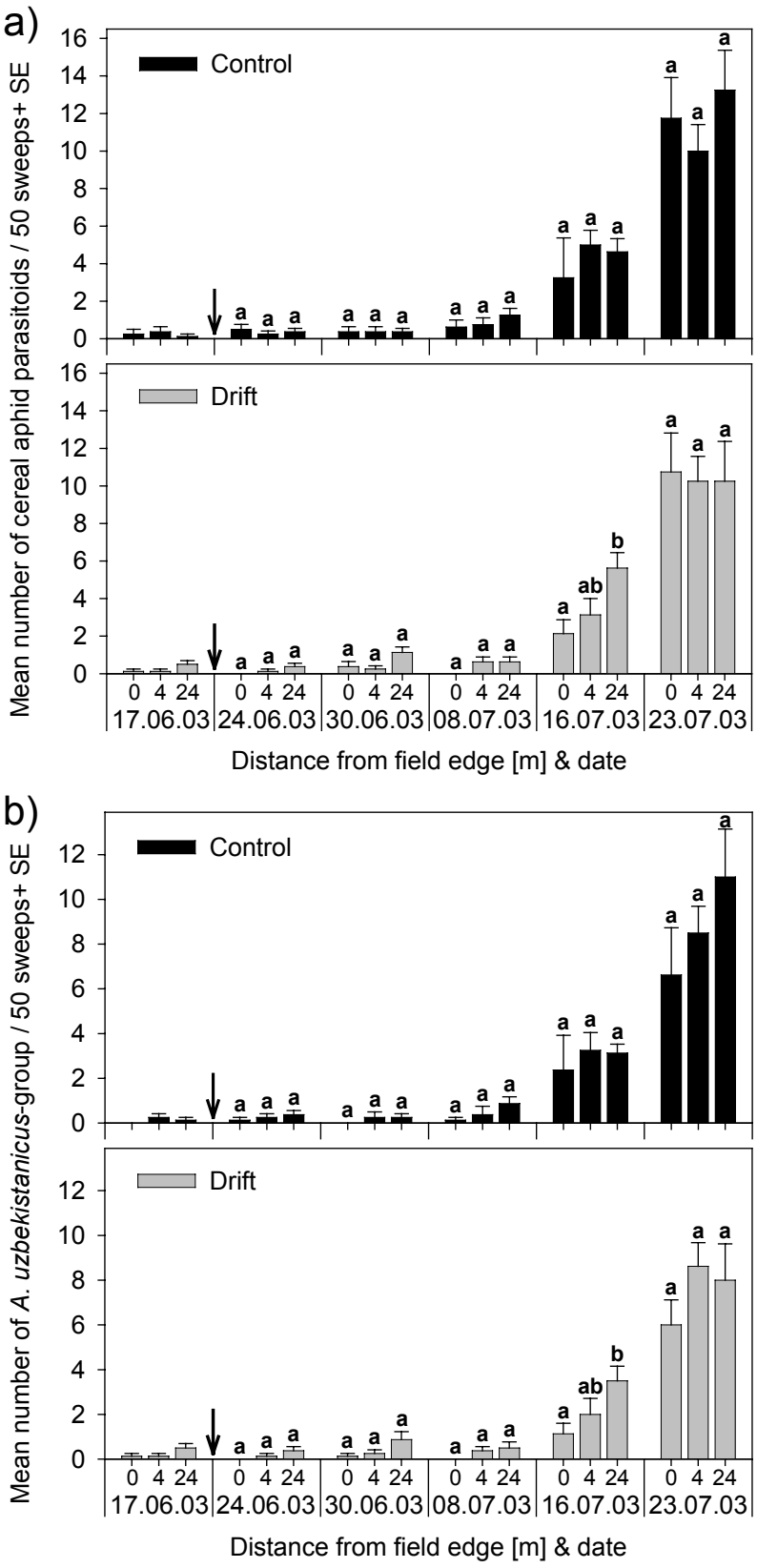

Fig. 32. Population development of **cereal aphid parasitoids** (a) and the ***A. uzbekistanicus*-group** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

On June 24, subsequent to the insecticide application, numbers of **adult *C. carnea*** in control plots levelled of in the field margins and at 4 m from the field edge, respectively, but decreased at 24 m into the wheat, when compared with pre-treatment densities (Fig. 33a). At the same time population densities of *C. carnea* decreased at all drift plot distances; no adult chrysopids were captured at 4 and 24 m into the wheat. On 30 June a sharp increase in numbers of adult lacewings was observed at each control- and drift plot-distance. There were no significant differences in densities among distances (Fig. 33a). On 8 July significantly more adult lacewings were captured in drift field margins than at 24 m into the wheat, whereas in control plots, no significant differences in population densities between distances were observed. On 16 July there was a decline in chrysopid population densities at all distances in both control and drift plots, with no significant differences in densities among distances. Finally, on 23 July numbers of *C. carnea* increased again; population densities were similar to those recorded on 30 June and 8 July, respectively, in both control and drift plots (Fig. 33a). No significant differences in densities of adult chrysopids were detected between distances.

Compared to pre-treatment densities lower numbers of **chrysopid larvae** were captured at all control and drift plot distances on 24 June (Fig. 33b). On 30 June population densities in control field margin strips exceeded the pre-treatment densities, whereas at all other positions in both control and drift plots numbers of chrysopid larvae had not recovered to pre-treatment densities. Numbers of lacewing larvae captured in control field margins were significantly higher than at 24 m into the wheat; this was the only significant difference in population densities detected between distances. On 8 July numbers of chrysopid larvae in drift plots increased evenly at all distances. In control plots an increase in densities was just observed in field margin strips, resulting in significantly higher densities in field margins than at 4 and 24 m from the field edge. However, on 16 July populations of chrysopid larvae increased to similar densities at all distances in both control and drift plots. Finally, numbers of lacewing larvae increased to an average of 11.8/50 sweeps (control) and 13.5/50 sweeps (drift), respectively, at 4 m and to an average of 17.0/50 sweeps (control) and 13.1/50 sweeps (drift), respectively, at 24 m from the field edge on 23 July. Within-field densities in control and drift plots, respectively, were significantly higher than off-field densities (Fig. 33b).

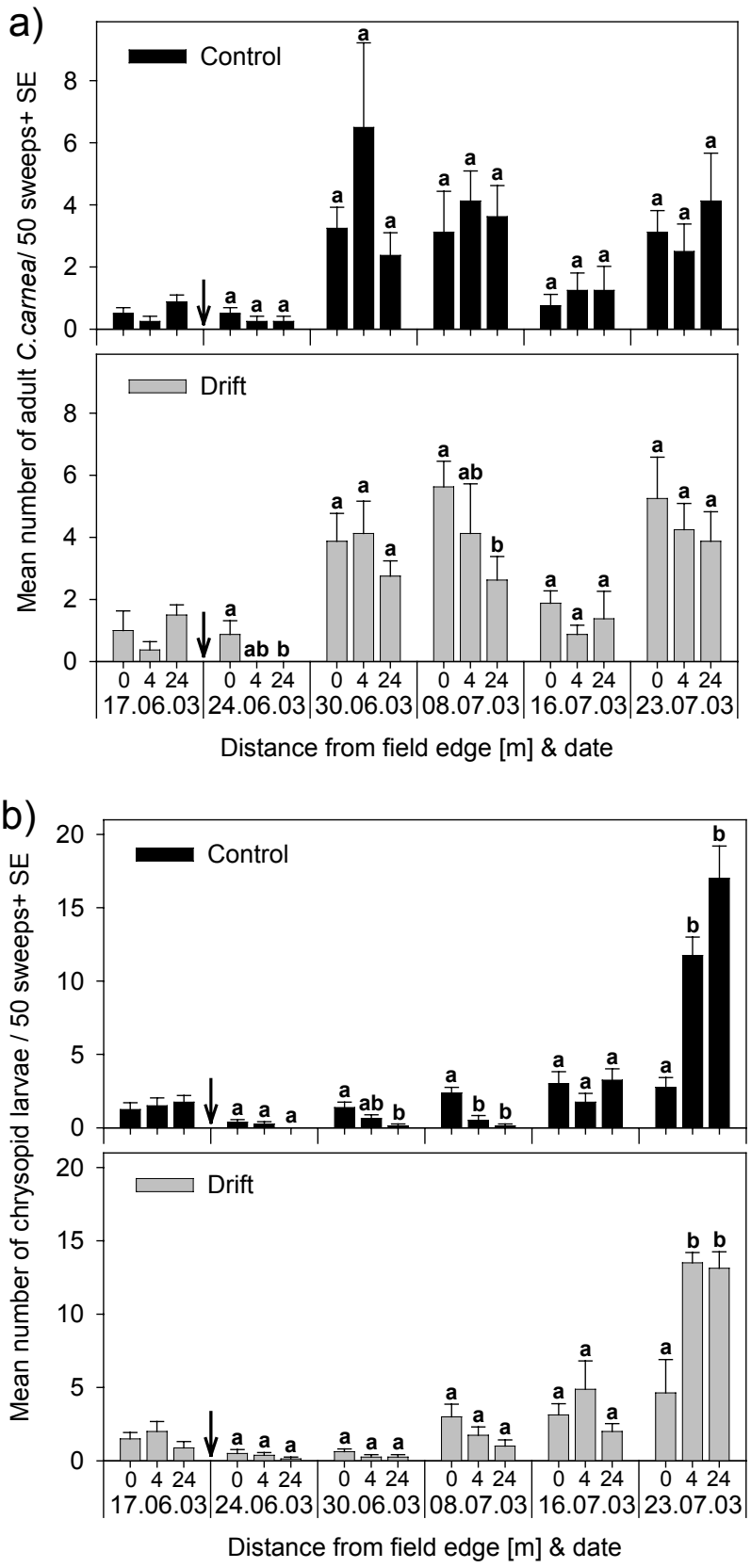

Fig. 33. Population development of **adult *C. carnea*** (a) and **chrysopid larvae** (b) at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

Prior to the application of λ-cyhalothrin to wheat fields most aphidophagous **coccinellids** were captured in field margin strips, few at 24 m, and not any at 4 m into the wheat in control and drift plots, respectively (Fig. 34). On 24 June, subsequent to the insecticide application, numbers of coccinellids decreased at all distances compared to pre-treatment densities in both control and drift plots; no specimens were captured in wheat areas at 4 and 24 m from the field edge (Fig. 34). Significantly more coccinellids were captured in control field margin strips than at 4 and 24 m from the field edge, whereas coccinellid densities in drift field margins were not significantly different from those at 4 and 24 m into the wheat. From 30 June to 16 July few coccinellids (mean ≤ 0.5 specimens/50 sweeps) were captured in control field margins. On two occasions specimens were recorded at 4 m (30 June) and 24 m (16 July). At the same time no coccinellid was collected at 4 and 24 m, respectively, in drift plots. Mean numbers of specimens caught in drift field margin strips were similar to those captured in control field margins. Finally, on 23 July coccinellids were captured at each control plot distance (Fig. 34). Population densities in control field margins exceeded pre-treatment densities and were significantly higher than those at 4 and 24 m into the wheat. In drift plots coccinellids were caught in the field margin and in wheat areas at 4 m, but not at 24 m from the field edge. Coccinellid densities in drift field margins nearly recovered to pre-treatment densities. There was no significant difference between coccinellid numbers in drift margins and those at 4 m from the field edge.

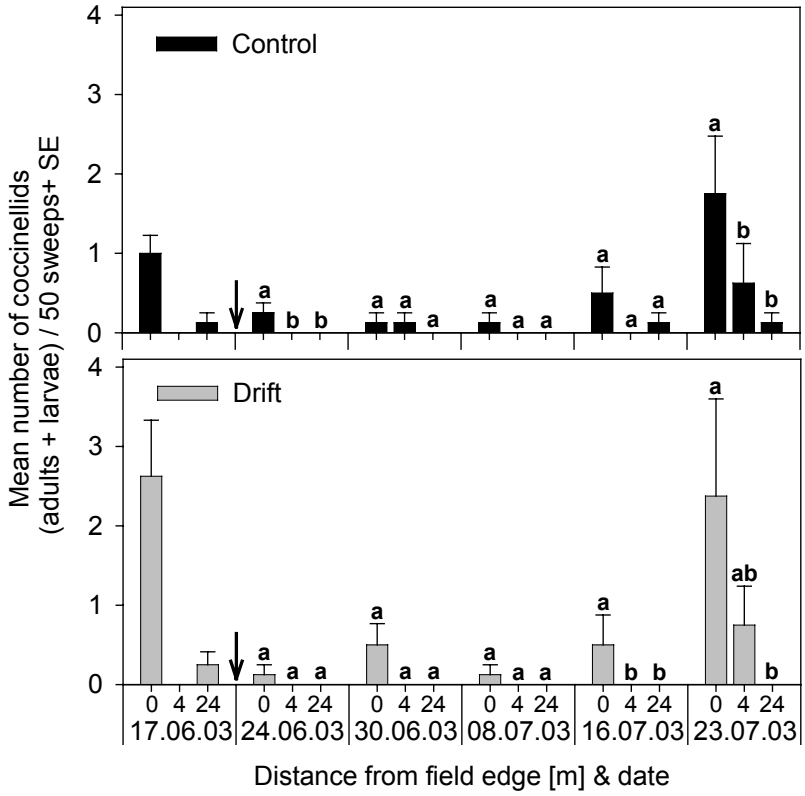

Fig. 34. Population development of **aphidophagous coccinellids** at different distances from the field edge before and after the insecticide application. The upper graph (lower graph) shows means (+ SE) within control (drift) field margin strips (i.e. 0 m) and in adjacent wheat areas at 4 and 24 m from the field edge. The arrow indicates date of insecticide application to the wheat. Different letters indicate significant differences ($p < 0.0167$) in post-treatment population densities among distances per date. Results of ATS are given in table A4, appendix.

3.4 DISCUSSION

3.4.1 Effect of λ-cyhalothrin drift on the population development of aphids

Being the target pest, aphids are highly sensitive to λ-cyhalothrin (anonymous, 2000b, 2001). Due to the non-systemic action of λ-cyhalothrin, drift effects on cereal aphids may have been caused predominantly by direct contact with drifting particles at the time of the application. Considering the relatively nonmobile phloem-feeding behaviour of aphids, indirect effects, e.g. insecticide uptake while walking on dried drift deposits on plant surfaces, might have been rather low (McGregor & Mackauer, 1989; Longley & Jepson, 1997b).

The effect on aphids, although being the target pest, may be indicative of the potential direct impact of drifting droplets on non-target arthropods with equal levels of susceptibility towards λ-cyhalothrin, e.g. linyphiid and lycosid spiders and mites (anonymous, 2000b). However, by extrapolating treatment effects to populations of other species not only species sensitivity towards insecticides has to be considered but also species behaviour, mobility, and diel activity pattern (e.g. Stark et al., 1995). The sensitive linyphiid spiders, for example, might be affected by insecticide drift via various routes. They can be directly affected by contact with airborne particles during application. Due to their mobility Linyphiidae might be negatively influenced by contact to dried drift deposits on plant or soil surfaces (Dinter, 1995). Furthermore, they are endangered by drifting particles that are collected in their webs (Samu et al., 1992) or by ingestion of their contaminated webs or prey (Dinter, 1995; Stark et al., 1995; Pekár, 1999).

After direct insecticide spray applications to cereal crops aphids feeding on lower leaf surfaces have often been found to be protected during spray applications (e.g. Niehoff, 1995; Longley & Jepson, 1997a) due to significantly lower insecticide deposition on lower compared to upper leaf surfaces (Cilgi & Jepson, 1992). However, as pointed out previously (2.4.1, page 25 et seqq.), the interception process of insecticide spray on in-crop plants during an insecticide application is different from the deposition of drifting droplets on off-crop plant surfaces (Koch et al., 2004b). Within a closed vegetation airflows carrying drift particles travel along meandering trajectories due to turbulence and lose drift particles by deposition on moving plant elements (Raupach et al., 2000). Plants are subjected to sudden changes of wind speed or direction, which may result in permanently changing positions of leaves, making the interception of pesticide drift in natural vegetation a very complex and random process (e.g. Koch et al., 2004a,b). As

a result, although in the current study aphids were frequently found feeding on abaxial leaf surfaces, these supposedly less exposed feeding sites seemed not to protect aphids from insecticide drift.

Drift effects on aphid population densities were transitory. Fast recoveries in aphid populations after insecticide treatments are explained by their life-history variables. Aphids have high intrinsic rates of increase, short generation times, and a short time interval for first offspring. For that reason they are supposed to be less susceptible to insecticides at population level than species with longer generation times, lower reproductive rates, and intrinsic rates of increase, such as the ladybeetle *C. septempunctata* (Stark & Banks, 2003; Stark et al., 2004a,b).

3.4.2 Effect of λ-cyhalothrin drift on the population development of syrphids

No effects of λ-cyhalothrin drift into field margins on total numbers of aphidophagous hoverflies, numbers of *E. balteatus*, *E. corollae*, *M. mellinum*, and *S. scripta*, respectively, as well as numbers of syrphid eggs deposited on wheat tillers were detected in the current study. The non-detectability of drift effects on population densities of adult syrphids seems to be connected with the high mobility of this group, which enables rapid recolonisation of treated crops from sheltered habitats (Candolfi et al., 2004). Additionally, adverse effects of insecticide applications on hoverflies may be very short-lived. This was indicated by a study of Markova & Ljubenova (1998), where the application of the synthetic pyrethroid α-cypermethrin to tomato fields initially (one day after treatment) reduced densities of syrphid flies, but populations numerically recovered by the fifth day after application. In the current study the first post-treatment sweep catches were done between 3 and 5.5 days after application, respectively, and therefore may have been too late to detect initial treatment effects on population densities of aphidophagous syrphid flies. In addition, in 2003 a sudden increase in aphidophagous hoverfly densities after the application complicated the detection of possible treatment effects. The observed increase in syrphid densities may have been the result of seasonal immigration and/or mass hatch from the pupal stage of the species *E. balteatus* and *E. corollae* (Gatter & Schmidt, 1990; Krause, 1997), which constituted 94 % of catches. Sudden population increases in aphidophagous syrphid species are not unusual and have previously been reported (e.g. Krause, 1997; Sutherland et al., 2001a).

Trafo® is classified as moderately toxic to populations of *E. balteatus* (BVL, 2003). In laboratory tests λ-cyhalothrin (5 g a.i./ha) caused 100 % mortality to *E. balteatus* larvae (L2) within 24 hours of exposure to deposits on leave surfaces (Colignon et al., 2003). The exposure of 2 to 3 days old larvae to λ-cyhalothrin deposits on glass plates caused 78 % corrected mortality (Jansen, 1998). Females that hatched from surviving larvae just laid non-viable eggs. However, due to low pre-treatment abundances in both study years it was not possible to estimate effects on adult *E. balteatus* in the current work.
To our knowledge, no LD_{50} values for λ-cyhalothrin and syrphid larvae or adults have been published so far. Due to this lack of data we cannot assess possible risks posed by drift deposits measured in the current study to syrphid life stages. Furthermore, no published data on the toxicity of λ-cyhalothrin on *E. corollae*, *M. mellinum*, and *S. scripta* are available so far.

3.4.3 Effect of λ-cyhalothrin drift on aphid mummy densities and on the population development of cereal aphid parasitoids

Following the insecticide treatment in 2002 no initial reduction of aphid mummy densities was detected both within-field and in the field margin strips. Suggesting an approximate developmental time from oviposition to mummification of most cereal aphid parasitoids of more than eight days under the given field conditions (Hågvar & Hofsvang, 1991; Sigsgaard, 2000), each mummy that was counted at the first post-treatment date (3/4.5 days p.a.) resulted from a pre-treatment oviposition. Therefore, the first post-treatment mummy count could just detect the toxic effect of λ-cyhalothrin on early immature parasitoid stages, i.e. on aphids that contain the immature stage but which were not mummified at the time of the insecticide spray. In laboratory experiments λ-cyhalothrin (6.25 g a.i./ha) caused 100 % mortality to both recently parasitised and non-parasitised *S. avenae* (Krespi et al., 1991). No published information is available on the risks posed by λ-cyhalothrin to recently parasitised *R. padi* and *M. dirhodum*. However, in addition to the negative drift effects that were observed on cereal aphid population densities (cf. 3.4.1), it might be suspected that λ-cyhalothrin drift also affected parasitised (but not yet mummified) cereal aphids, resulting in a decline in mummy densities in drift contaminated field margins subsequent to the application. However, observations made in the current study did not indicate an effect of insecticide drift on mummy densities. There are several reasons for the non-detectability of drift effects. First, each mummy count was based on a

population of different-aged mummies. Theoretically, although unlikely, all mummies that were found on the first post-treatment count had already been mummified at the time of the insecticide spray, thereby masking treatment effects. Second, as a result of the death of immature parasitoids inside the mummified aphids an accumulation of mummies could have occurred, resulting in an overestimation of mummy densities. However, results from laboratory toxicity studies indicated that λ-cyhalothrin poses a low risk to the immature parasitoid during late mummy stages, thereby rebutting the last assumption. In laboratory studies λ-cyhalothrin neither influenced the hatch of *A. uzbekistanicus* from mummified *S. avenae* (Krespi et al., 1991) nor the hatch of *A. rhopalosiphi* from mummified *S. avenae* and *M. dirhodum*, respectively (Jansen, 1996).

A more precise but also more labour-intensive method of measuring insecticide effects on parasitoid performance in the field is the estimation of parasitation or mummification rates. In 2003, within the scope of his diploma thesis, Mark Fiedler estimated the mummification rate of cereal aphids in the experimental field plots. Based on the collection of living aphids and the subsequent rearing in the lab until mummy formation, the mummification rate was calculated. The late immigration of cereal aphid parasitoids in 2003 resulted in 0 % (± 0 % SE) pre-treatment mummification rate both within-field and off-field. The first post-treatment estimation of mummification rates of aphids in field margins was done ten days after the application, i.e. too late to detect initial drift effects. However, at that time no effects of insecticide drift on mummification rates of cereal aphids were observed when compared with the control (t-test: $df = 6$, $t = 0.28$, $p = 0.791$) (Fiedler, unpublished).

Mummy densities estimated approximately ten days subsequent to the insecticide application could theoretically reflect effects of the insecticide treatment on density or activity of cereal aphid parasitoids during the first days after the application. However, due to the temperature-dependent several days´ duration of the preimaginal development of cereal aphid parasitoids (Elliott et al., 1995; Sigsgaard, 2000), each count was based on a population of different-aged mummies. Consequently, just very strong and persistent treatment effects on parasitoids may be reflected by reduced mummy densities.

In 2002 no significant effects of λ-cyhalothrin drift on total cereal aphid parasitoids and the *A. uzbekistanicus*-group, respectively, were detected in the current study. However, statistical analysis of drift effects on parasitoids can be open to misinterpretation when treatment effects are analysed at family or functional group level instead of species level. By the first post-treatment sweep sample more, though statistically insignificant,

cereal aphid parasitoids were collected in control field margins compared to insecticide drift-contaminated field margins. However, this trend was not observed when the analysis was conducted at species level for the most frequently captured aphid parasitoid species group, the *A. uzbekistanicus*-group. However, the analysis of insecticide effects on individual parasitoid species is limited by several factors. First, the accurate identification of specimens to species level can be difficult. In the current study, for example, it was problematic to definitely separate *A. rhopalosiphi* and *A. uzbekistanicus*, therefore they were pooled to the *A. uzbekistanicus*-group, as done in previous studies (e.g. Powell, 1982; Langer, 2001). Second, specimens belonging to individual species are often collected in very low numbers that do not allow reasonable statistical analysis (see below, 3.4.11). Third, interpretation of treatment effects at the species level is often limited by the lack of published data on species ecology or on their sensitivity to certain insecticides.

The fact that no significant drift effects were observed on population dynamics of cereal aphid parasitoids in field margins corroborates results of the exposure bioassays using *A. colemani* Viereck (cf. 2.3.3). In terms of mortality, these bioassays indicated that λ-cyhalothrin drift deposits on bean leaf surfaces were slightly to moderately harmful to *A. colemani* (based on the evaluation categories by the IOBC/WPRS-working group "Pesticides and Beneficial Organisms" (e.g. Sterk et al., 1999)). Twelve hours after exposure to drift deposits on leaf surfaces at 1 to 3 m from the field edge, corrected mortalities of *A. colemani* were < 20 %. Within the subsequent 12 hours of exposure mortalities of *A. colemani* slightly increased; just in few replicates mortality rates did exceed 50 %. However, as previously mentioned (2.4.1), the usually high variability in spray drift deposits on off-crop plant surfaces results in highly variable exposure scenarios, making it difficult to assess real risks posed by insecticide drift at definite distances from the field edge (Koch et al., 2003). This is supported by the study of Kühne et al. (2002), who calculated mortality levels of *A. rhopalosiphi* based on real spray drift deposit pattern within field margins. As a result, mortality > 50 % for *A. rhopalosiphi* was likely to occur at a distance of 1 m from the field edge. At farther distances the risks for this parasitoid species were found to be lower, although drift deposit pattern showed that peak deposits may cause > 50 % mortality up to a distance of 5 m from the sprayed field.

However, as previously pointed out (2.4.5), laboratory exposure assays can be regarded as worst-case scenarios, since test organisms are forced to have continuous contact with insecticide deposits. While searching for hosts or mates in the field parasitoids will come into contact with different deposits on plant surfaces. Furthermore they might be able to avoid contact with treated surfaces, though there were no

indications of repellent effects of λ-cyhalothrin on *A. rhopalosiphi* (Jansen, 2001) as well as on *A. colemani* in the current study. On the other hand, parasitoids might be heavily affected during the insecticide spray when hit by drifting droplets. However, so far no published information is available regarding the direct exposure of aphid parasitoids to insecticide spray drift.

Although data from toxicity studies using *A. colemani* indicated that drift effects on cereal aphid parasitoid population densities could be expected, no significant differences in population dynamics among control and drift contaminated field margin strips were detected. This is probably explained by rapid population recovery following the insecticide spray. Recovery of parasitoids is supposed to rely on two sources (e.g. Longley et al., 1997b), first, the emergence of adults from mummies, which offer protection against λ-cyhalothrin (Krespi et al., 1991; Jansen, 1996), and second, population recovery by reinvasion of parasitoids from surrounding habitats. Since experimental fields were embedded into an intensively cultivated agricultural landscape with large areas of winter wheat, these crops might have harboured reservoir populations. However, these assumptions are purely speculative; the presence of source populations in adjacent (winter wheat) fields has not been investigated in the current study.

For future studies on the effects of insecticide drift on aphid parasitoid population dynamics it is recommended to estimate post-treatment population densities in shorter time intervals. To detect initial drift effects on aphid parasitoid populations, the first post-treatment sample ideally should be taken few hours following the insecticide treatment. However, this was not realisable in the current study because of the complex actions associated with the drift deposit measurements and the exposure bioassays.

3.4.4 Effect of λ-cyhalothrin drift on the population development of chrysopids

In 2003 no effects of insecticide drift on population densities of chrysopid larvae in field margins were observed. Mean drift deposits of λ-cyhalothrin on leaf surfaces of broad beans exposed within field margin strips during the application were < 0.7 ng/cm² at ear-height and ground-level, respectively. Thus, deposits were more than 180-fold lower than the LR_{50} value for *C. carnea* (Stephens) larvae on natural substrates (112.26 ng λ-cyhalothrin/cm²), estimated in standard laboratory testing (Kühne et al.,

2002). The relatively low susceptibility of Chrysopidae towards λ-cyhalothrin has been confirmed by previous studies. Candolfi et al. (2004) did not find negative effects of Karate express (λ-cyhalothrin) treatment (10 g a.i./ha) on population densities of chrysopids (adults and larvae pooled) in corn. In standard laboratory glass plate tests λ-cyhalothrin caused low mortality (< 30 %) to *C. carnea* larvae (Sterk et al., 1999). In Germany, Trafo® is classified as non-toxic to populations of *C. carnea* (BVL, 2003).

3.4.5 Effect of λ-cyhalothrin drift on the population development of coccinellids

The effect of λ-cyhalothrin drift on Coccinellidae was not unexpected since previous laboratory and field studies have shown the high susceptibility of different coccinellid species and stages to this insecticide (cf. section 2.4.3 and Niehoff, 1996; Sterk et al. 1999; Tillmann & Mulrooney, 2000; Wick & Freier, 2000; Ba M´hamed & Chemseddine, 2002; Musser & Shelton, 2003).

Until now, just one other study analysed the effects of λ-cyhalothrin spray drift on coccinellids. Kühne et al. (2002) reported possible high risks of λ-cyhalothrin drift deposits to adult *C. septempunctata*. By comparing λ-cyhalothrin spray drift deposit pattern with mortality data from laboratory testing they identified areas within field margins with a potential risk of mortalities > 50 % for adult *C. septempunctata*. Drift pattern showed that the presence of such “hot spots” with > 50 % ladybeetle mortality might be possible at any distance within a field margin up to 5 m from the field edge. However, due to low coccinellid population densities, their field observations could not validate the theoretical predictions with empirical data.

In the first part of the current work (cf. 2.3.4) the toxicity of λ-cyhalothrin drift deposits on plant surfaces to *C. septempunctata* larvae was estimated by exposure bioassays. Therefore broad bean plants, acting as natural drift collectors, were deployed at 1, 2 and 3 m from the field edge within the field margin strips. Immediately after the insecticide application plants were removed from the field and test-organisms were exposed to dried deposits on adaxial leaf-surfaces. Ladybeetle larvae showed a rapid reaction towards deposits resulting in high mortalities (mean ≥ 58 %) within three hours after exposure on plants exposed to drift at 1 m distance from the field edge and on plants exposed within the wheat fields. Increasing the duration of exposure to 12 hours caused an increase in mortality levels of *C. septempunctata* larvae. Depending on deposits, mortality of larvae increased to > 50 % on plants exposed to drift at up to 3 m

from the field edge. Exposure to within-field spray deposits caused mortalities of nearly 100 % to ladybeetle larvae. The comparison of LR_{50} values for adult *C. septempunctata* (1.74 ng/cm² (Kühne et al., 2002)) and deposits of λ-cyhalothrin measured on leaf surfaces of broad beans indicated that mortality risks for the adult stage might also have been high within-crop and at short distance from the field edge.

The effect a pesticide will have on a field population of organisms does not only depend on the inherent susceptibility of specimens, but also on their exposure to the product, which is closely connected with species-specific biology and behaviour (Stark et al., 1995). Due to their mobility and predatory activity (Hodek & Honěk, 1996) pesticide effects on Coccinellidae may be caused by several routes of exposure, i.e. direct contact with drifting insecticide particles during the application, contact to dried deposits on plant or soil surfaces, or ingestion of contaminated food. In addition to mortality, sublethal effects on the behaviour or the mobility of coccinellids might also have accounted for significantly reduced numbers recorded in λ-cyhalothrin contaminated areas in the current study. Provost et al. (2003) found that sublethal deposits of λ-cyhalothrin on leaf surfaces significantly reduced both the time spent moving and the velocity of exposed ladybeetle larvae (*Harmonia axyridis* (Pallas)). Furthermore, repellent effects could have resulted in the avoidance of coccinellids to feed or stay in areas treated with λ-cyhalothrin. However, field observations of Studebaker et al. (2003) did not indicate repellent activity of λ-cyhalothrin towards coccinellids. Additionally, in exposure bioassays we did not find evidence for repellent effects of λ-cyhalothrin on *C. septempunctata* larvae, as test organisms were frequently found on treated leaves.

3.4.6 Aphid population recovery in wheat areas adjacent to drift-contaminated and drift-protected field margins

First post-treatment aphid monitoring indicated significantly higher cereal aphid population densities in wheat areas at close distance (4 and 5 m, respectively) from control field margin strips than at farther distance (24 and 25 m, respectively). Since post-treatment aphid densities were higher, although not always significantly, in control field margins than in the wheat crop, field margin strips possibly acted as a source of “aphid colonists” that immigrated into the adjacent crop. The significant difference in aphid densities between 5 and 25 m (and 4 and 24 m, respectively) was transitory,

indicating a redistribution of aphid populations within the wheat (Duffield & Aebischer, 1994) approximately two weeks following the insecticide application.

Contrary to control plots, subsequent to the insecticide application aphid densities in drift plot wheat areas at 5 m (4 m) were not significantly higher than those at 25 m (24 m). This finding suggests that no invasion of aphids from drift-contaminated field margin strips into the wheat occurred, or at least not to the same extent, as in control plots. A possible explanation for this discrepancy might be the difference in aphid densities between control and drift field margin strips. As seen by pairwise comparisons, λ-cyhalothrin drift had a (sometimes significant) negative effect on aphid population densities in drift field margins, resulting in lower initial post-treatment aphid densities in drift field margin strips compared to control field margin strips. Therefore, fewer potential colonists were present in drift field margins. Furthermore, λ-cyhalothrin might have affected the mobility of aphids, resulting in reduced dispersal in aphids. Lambda-cyhalothrin has been shown to reduce the mobility of ladybeetle larvae (Provost et al., 2003).

Unexpectedly, the spatial trend in cereal aphid recovery/reimmigration in control plots was just observed at the functional group level, but it was never observed at the species level. As a result, assumptions concerning the reimmigration of cereal aphids from control field margin strips into the wheat should be treated with some caution.

An earlier Dutch study investigated the migration of aphids from insecticide sprayed and unsprayed wheat field edges into the adjacent crop (de Snoo & de Leeuw, 1996). Although high aphid densities were found in the unsprayed field edges, scientist did not find significantly higher aphid densities among wheat areas bordering unsprayed field edges and those bordering sprayed edges, even at a distance of 2 m into the wheat.

Although alate aphids occurred in higher densities in field margin strips, data did not indicate that alate aphids reimmigrated from the field margins into the wheat subsequent to the application. Furthermore, control and drift field margins did not appear to differently influence aphid densities in the wheat areas at 4 and 24 m from the field edge. However, winged aphids were not identified to the species level. Therefore, it is suspected that a large amount of field margin-catches were “indifferent” alate aphids that did not feed on wheat but on other plants species that were available in the margins.

Earlier studies investigated the spatial recovery of cereal aphids following the application of the pyrethroid insecticide deltamethrin in winter wheat. Longley et al. (1997a) analysed the spatial recovery of *S. avenae* subsequent to the application of a full-rate and a reduced-rate (i.e. -80 %) treatment. Aphid densities were initially

reduced by 78 % (full-rate) and 40 % (reduced-rate), respectively. In the full-rate treatment no significant gradients in spatial aphid population recovery were found. This was explained by a spatially random pattern of survival. In the reduced-rate treatment initial recovery of *S. avenae* occurred most rapidly in the centre (i.e. > 40 m from field edge) of the treated plots. Scientists did not provide an explanation for this result, but referred to the study of Duffield & Aebischer (1994), who also found indications for a post-treatment recovery of cereal aphids that was most rapid in the centre of a treated wheat field. For the predatory groups Carabidae, Staphylinidae and Linyphiidae the latter study showed a contrary spatial recovery, which progressed from the edge to the centre of the field. Scientists concluded that the observed spatial pattern of aphid resurgence was attributed to the difference in predation pressure between field edge and field centre.

There may be two reasons for the different outcomes of the present study and the study by Longley et al. (1997a). First, due to the sown wheat transects, aphid densities in the field margin strips of the current study were (artificially) high and could therefore have acted as a source of colonists. The source of potential colonists in the study of Longley et al. (1997a) was comparatively low. The insecticide treated experimental field plots were surrounded by insecticide free control areas with means of < 2 aphids/ear. Second, Longley et al. (1997a) conducted aphid counts at 20 to 100 m from the field edge, i.e. their study was not designed to detect aphid immigration on a small spatial scale. However, as mentioned before, no indications for an immigration of cereal aphids from the field margin into the wheat were detected at the species level. All assumptions concerning the reimmigration of aphids should therefore be treated with caution.

In 2002 aphid densities in field margin strips as well as in the wheat fields declined in July and did not recover to pre-treatment levels until harvest. Aphids were obviously affected by three heavy rainfall events in mid July (20, 23, and 72 mm (!) rain/day), which caused lodging of the wheat and the field margin strips.

In 2003 resurgence in cereal aphid populations occurred approximately three weeks subsequent to the insecticide application. Weather conditions were generally favourable during the weeks subsequent to the insecticide application, with no extremes of temperatures, precipitation, or wind. A large increase in densities of alate aphids in mid July seemed to indicate the migration of cereal aphids out of the crop. In late July, aphid densities declined at all distances. At that time numbers of cereal aphid parasitoids, chrysopid larvae, and aphidophagous coccinellids peaked.

3.4.7 Syrphid population recovery in wheat areas adjacent to drift-contaminated and drift-protected field margins

In both study years pre-treatment densities of adult syrphids were very low, with some species being absent in pre-treatment sweep catches. Numbers sharply increased subsequent to the application (possible explanations for the sudden population increase are given above, 3.4.2). Therefore, immigration rather than reimmigration into field plots subsequent to the insecticide application could be analysed. Overall, spatial distribution of hoverflies was relatively homogenous during the 2002 and 2003 monitoring periods, with almost always significantly higher syrphid densities in field margins than in adjacent wheat areas in both control and drift field plots. This trend was observed at functional group and species level, respectively. Furthermore, densities of hoverflies were frequently found to be significantly higher at 4 than at 24 m from the field edge. This decrease in numbers with distance into the field might be indicative of a temporary migration of aphidophagous syrphids between field margins and the adjacent crop where they search for aphid colonies in which to oviposit (White et al., 1995; Bowie et al., 1999; Sutherland et al., 2001a,b). High aggregations of aphidophagous hoverflies in field margin habitats with floral resources have been shown in previous studies (e.g. Frank, 1999; Sutherland et al., 2001a). The attraction of adult syrphids to these habitats relies on their dependence on nectar as carbohydrate source and pollen, which is essential for egg maturation (e.g. Hickman & Wratten, 1996).

Spatial patterns of syrphid densities following the insecticide application did not differ greatly between control and drift field plots, i.e. control and drift-contaminated field margin strips did not differently influence syrphid densities in wheat. Analysis of drift effects (cf. 3.3.5 & 3.4.2) showed that post-treatment hoverfly numbers at functional group and at species level, respectively, did not differ between control and drift field margins. So, both margin types harboured similar numbers of potential colonists.

Analysis of syrphid egg distribution in 2002 also suggests that control and drift-contaminated field margin strips did not differently influence syrphid egg densities in wheat areas at 5 and 25 m from the field edge. In contrast to numbers of adult syrphids that decreased with distance into the field, this trend was not observed in egg distribution in both control and drift plots. Statistical analysis of the first post-treatment count revealed that numbers of syrphid eggs on wheat tillers were significantly influenced by aphid densities but not by the distance from the field edge. This result demonstrates the importance of host availability for a (re)invasion of syrphids into fields following an insecticide treatment. Furthermore, it might reflect the positive density-

dependent oviposition in *E. balteatus* (Bargen et al., 1998; Sutherland et al., 2001b), that was the second most abundant species in field plots in 2002. As aphid densities declined, eggs seemed to be deposited independently of aphid numbers.

Results of the current study suggest that aphidophagous syrphids might be a suitable indicator group for the estimation of insecticide drift effects on highly dispersive non-target arthropod populations. Furthermore, they may be used in future studies on post-treatment reimmigration processes from field margin habitats into a field crop. Firstly, they are positively associated with floral resources in field margins, which offer food sources (i.e. pollen and nectar, see above); within these margins syrphids can reach high population densities (MacLeod, 1999; Sutherland et al., 2001a). As previously mentioned, this is an important prerequisite for the application of statistical tests. Secondly, syrphids migrate temporarily between field margins and the adjacent crop (Ruppert, 1992; White et al., 1995; Bowie et al., 1999; Sutherland et al., 2001a). For an analysis of reimmigration at species level, the three species *E. balteatus*, *M. mellinum*, and *E. corollae* might be equally suitable indicator species, as they were almost always captured in the field margins and at 4 and 24 m into the wheat. In contrast, *S. scripta* appeared to be confined to field margins. However, because of the very small numbers of *S. scripta* caught, this assumption must be treated with caution.

3.4.8 Recovery of cereal aphid parasitoid populations in wheat areas adjacent to drift-contaminated and drift-protected field margins

Spray deposit measurements yielded mean deposits of λ-cyhalothrin on within-crop top-leaves from 5.04 to 8.24 ng a.i./cm² leaf surface. These caused mean corrected mortalities from 35 % to 56 % to *A. colemani* exposed for 24 hours to deposits (cf. 2.3.3). Published LR_{50} values for two cereal aphid parasitoid species that were recorded at the experimental sites are 4.97 ng λ-cyhalothrin/cm² for *A. ervi* Haliday (Desneux et al., 2004) and 5.9 ng λ-cyhalothrin/cm² for *A. rhopalosiphi* (Kühne et al., 2002). In the absence of published information on LR_{50} values (λ-cyhalothrin) for the other parasitoid species that were recorded in the present study, similar sensitivity to λ-cyhalothrin among *Aphidius* species is assumed. However, since Maise et al. (1997) detected differences in the sensitivity to dimethoate among *A. colemani*, *A. rhopalosiphi*, and *A. matricariae* Haliday, we cannot totally rule out species-specific differences in sensitivity to λ-cyhalothrin within the order *Aphidius*.

LR_{50} values indicate that contact to deposits on plant surfaces could cause 50 % mortality to *Aphidius* species. However, since these values were determined under worst-case exposure conditions (i.e. 24 hours of exposure to λ-cyhalothrin treated glass surfaces), risks might be much lower under field conditions. This is supported by a study conducted under more realistic conditions (Jansen, 2001), where *A. rhopalosiphi* suffered just 11 % mortality within 24 hours of exposure to wheat plants treated with a reduced rate of λ-cyhalothrin of 5 g a.i./ha (current study 10 g a.i/ha (2002) and 7.5 g a.i./ha (2003)). The author explained the low mortality of wasps by non-continuous contact to treated surfaces due to their searching activity and their periodic flight behaviour. On the other hand, in the field parasitoids might be highly at risk during and shortly after the insecticide application when they can be directly hit by spray droplets or get in contact with fresh non-dry insecticide deposits. Furthermore, uptake of contaminated honeydew can be another source of exposure to insecticides in the field (Longley & Stark, 1996).

Considering these potential risks, it was surprising that in both study years no negative effects of the insecticide application on cereal aphid parasitoid population densities were detected. This might be explained by the natural population development in cereal aphid parasitoids. In 2002 parasitoid data were confounded by very low pre-treatment densities followed by a sudden increase in numbers (mainly due to the *A. uzbekistanicus*-group) at all sample positions after the insecticide application. In 2003 both pre- and post-treatment densities of aphid parasitoids were extremely low. Since parasitoid densities in untreated control field margin strips were as low as those in treated wheat areas and no differences in population dynamics between treated and untreated areas were detected, the application of λ-cyhalothrin seemed not to be the reason for the overall low abundance of cereal aphid parasitoids in 2003. Parasitoid populations increased not until 3.5 weeks subsequent to the application, when aphids peaked.

Overall, no spatial trend in cereal aphid parasitoid (re)invasion into wheat fields following the insecticide application was detected in both control and drift plots. Parasitoids appeared to be equally distributed amongst field margins and adjacent wheat areas. As a result, control and drift field margin strips did not differentially influence densities of parasitoids at 4 and 24 m into the wheat. Longley et al. (1997a) analysed the recovery/reimmigration of aphid parasitoids (mainly *Aphidius* spp.) following the application of deltamethrin in wheat fields. The insecticide caused initial (one day after treatment) reductions in parasitoid populations of 90 %, followed by a full recovery within 19 days after treatment. The spatial distribution of *Aphidius* spp.

indicated that initial recovery of populations was higher at the edges of the field compared with the centre. Scientists supposed that this pattern of recovery reflected the reinvasion by parasitoids from untreated surrounding habitats. After the application of a reduced rate (-80 %) of deltamethrin, initial reductions of parasitoid numbers were lower (60 %). Full recovery occurred within five days after treatment; no clear spatial pattern in population recovery was detected. However, data of that study should be treated with some caution as no replications were performed. Another published study is available that was designed to analyse the spatial recovery of aphid parasitoids following insecticide (dimethoate) application in wheat (Holland et al., 2000). However, since parasitoid populations did not recover after spraying, the study failed to provide information regarding reimmigration.

The different spatial patterns in recovery of parasitoids among wheat fields that received a reduced rate and a full rate of insecticide, which were detected by Longley et al. (1997a), suggest that statistical analysis of reimmigration processes following insecticide applications might be very difficult when initial treatment effects are relatively low, i.e. when a large number of specimens survive. Since survival is supposed to not show spatial patterning (Longley et al., 1997a), the detection of reimmigration might be masked by redistribution of survivors.

Owing to the fact that no reductions in aphid parasitoid populations following the spray were observed in the present work, we could not provide evidence that field margin strips acted as source of cereal aphid parasitoids that dispersed into the treated crop to contribute to repopulation. However, recent studies demonstrated that field margin strips, when providing alternative aphid hosts, attract and maintain cereal aphid parasitoids (Langer & Hance, 2004; Levie et al., 2004). Furthermore, these strips were shown to enhance parasitism of cereal aphids at least up to 45 m into adjacent wheat fields when compared with strip-free control fields (Levie et al., 2004). Based on published information (e.g. Fernandes et al., 1997; Muratori et al., 2000; Levie et al., 2004) and own observations on the dispersal capability of aphid parasitoids (cf. sections 4 and 5), it is suspected that the distance of individual parasitoid movement from field margin habitats into the wheat (and back?) ranges at least between 50 to 100 m, and probably much farther.

Aphid parasitoids were equally distributed among field margins and wheat areas in the current study. Our observations corroborate previous studies that also found *Aphidius* species to be evenly distributed across (insecticide-free) wheat fields (Longley et al., 1997a; Holland et al., 2000; Levie et al., 2004). In contrast to aphidophagous syrphids that are attracted to field margins with flowering sources since they rely upon pollen

and nectar (Sutherland et al., 2001a), cereal aphid parasitoids can complete their life cycle within the wheat crop. Because aphid honeydew is the essential food source in aphid parasitoids (Hågvar & Hofsvang, 1991), they can find both their food source and their aphid hosts within wheat fields. As a result, temporal migration between field margin and wheat field, as observed in syrphids (e.g. Ruppert, 1992; Sutherland et al., 2001a,b), might not be suspected in individual cereal aphid parasitoids (Longley et al., 1997a).

In contrast to adult parasitoids, aphid mummies appeared not always to be evenly distributed across field plots. Approximately ten days after the insecticide treatment in 2002, significantly higher mummy densities were found in control and drift field margins, respectively, compared with wheat areas at 5 and 25 m from the field edge. Given that the developmental time from egg to mummy took several days (cf. 3.4.3), it is suggested that the pattern of aphid distribution to some extent determined pattern of mummy distribution observed approximately ten days later. High aphid densities in field margins on the first two monitoring dates resulted in a high number of parasitism events (Hågvar & Hofsvang, 1991) and consequently in high mummy densities in subsequent counts. From 26 June 2002 (second post-treatment count) aphids were equally distributed among field plots, as were mummies from 9 July.

3.4.9 Chrysopid population recovery in wheat areas adjacent to drift-contaminated and drift-protected field margins

Three and four days, respectively, subsequent to the insecticide application in 2003 no adult *C. carnea* was captured in wheat areas at 4 and 24 m adjacent to drift contaminated field margins. At the same time, numbers in control plots were lower at 24 m into the wheat compared to pre-treatment densities. It might be suggested that the reduced within-field abundances observed in adult *C. carnea* following the spray might reflect the toxic effects of the insecticide towards chrysopids. However, *C. carnea* has a relatively broad tolerance to many insecticides (Bay et al., 1993), including λ-cyhalothrin, which is classified as harmless to populations of *C. carnea* (BVL, 2003). Therefore, it was not expected to detect strong direct treatment effects on chrysopids in the current study. More likely, the decline in numbers might have been an indirect effect of the insecticide. Since aphid honeydew and herbivore-induced plant volatiles (Bay et al., 1993; James, 2003) are known to act as kairomones for adult *C. carnea*,

which attract them to aphid infested plants, the decline in aphid population densities following the treatment might have caused reduced *C. carnea* densities in the wheat.
Ten days after the application, a sharp increase in *C. carnea* densities was observed in both field margins and adjacent wheat areas, with no significant differences among distances in control and drift plots, respectively. The fact that very low numbers of chrysopid larvae were detected on wheat tillers in the beginning of June (data not presented) suggests that the large increase in adults was due to immigration rather than to hatch from the pupal stage. During the first two to three days of their adult life, female *C. carnea* conduct long-distance migration flights and can cover an average distance of 40 km per night (Bay et al., 1993). Therefore, immigrating *C. carnea* were suspected to originate from various sources and not only from sown field margin strips.

Seeing that subsequent to the insecticide application no clear reduction in numbers of chrysopid eggs on within-field wheat tillers was observed, chrysopid egg densities did not indicate a negative effect of λ-cyhalothrin on the egg deposition by female lacewings. Under the given field conditions (over the whole monitoring period: average temperature 18°C, average humidity 70%) the egg incubation required approximately nine to 11 days (Bänsch, 1964). As a result, on each monitoring date egg counts were based on a population of different-aged eggs. Therefore, just very strong and persistent insecticide side-effects on adult chrysopids would have been reflected by reduced egg densities. The same dilemma has been described above for aphid mummies (cf. 3.4.8). Overall, the distribution and abundance of eggs over control and drift plots, respectively, seemed not to be correlated with the distribution of adult *C. carnea* or cereal aphids. This was especially evident on 7 and 14 July, respectively, where significantly fewer chrysopid eggs were recorded on wheat tillers in field margin strips than in wheat areas at 5 and 25 m from the field edge. At that time, *C. carnea* adults and cereal aphids were equally distributed among field plots, with no significant differences in abundances found among field margins and wheat areas. There might be several reasons for this; firstly, predation on chrysopid eggs in field margins was higher than in wheat fields. Secondly, sown wheat plants in the field margins were unattractive to female chrysopids. Thirdly, female *C. carnea* deposit their eggs virtually everywhere (e.g. Bay et al., 1993). In the current study, for example, dozens of eggs were found on the anemometer that was installed at the field edge. The queer egg-laying behaviour of *C. carnea* might be an important reason why no correlation was found.
Few days following the application of λ-cyhalothrin to the wheat numbers of chrysopid larvae decreased in field margins as well as at 4 and 24 m into the wheat in both

control and drift plots. Given the low toxicity of λ-cyhalothrin to chrysopid larvae and the decline in numbers in untreated control field margins, reduced densities did most likely not result from the insecticide application. Mean deposits of λ-cyhalothrin on leaf surfaces of broad beans exposed within wheat fields during the application were < 10 ng/cm² at ear height and < 2 ng/cm² at ground level, i.e. deposits were more than 10fold lower than the LR_{50} value for *C. carnea* larvae on natural substrates (112.26 ng λ-cyhalothrin/cm²), estimated in standard laboratory testing (Kühne et al., 2002).

Both in 2002 and 2003, chrysopid larvae were equally distributed among field margins and adjacent wheat areas, with just few significant differences between distances. However, the last monitoring date in 2003 revealed significantly higher larval densities at 4 and 24 m into the wheat compared with field margins in control and drift plots, respectively. Since the distribution of larvae appeared to reflect the distribution of chrysopid eggs observed during earlier counts, it can be assumed that the high numbers of larvae captured in wheat fields were associated with hatch from these eggs rather than with immigration from surrounding habitats. However, laboratory experiments showed that *C. carnea* larvae are able to disperse 214 m without water or food (Bay et al., 1993). Hence, immigration of chrysopid larvae might also have occurred.

3.4.10 Coccinellid population recovery in wheat areas adjacent to drift-contaminated and drift-protected field margins

In the current study the application of λ-cyhalothrin totally reduced within-field densities of aphidophagous coccinellids for a period of approximately three weeks. This relatively long-lasting reduction may not only reflect the high acute toxicity of λ-cyhalothrin and its persistent harmful activity (e.g. Sterk et al., 1999) but it possibly also indicates the comparatively low recovery potential of coccinellids. Stark & Banks (2003) and Stark et al. (2004a,b) suggested that due to their relatively low population growth rate, their long generation time, and their high numbers of developmental stages coccinellid populations might generally be more susceptible to pesticides than populations of aphids and aphid parasitoids.

During the first three weeks after the application of λ-cyhalothrin, coccinellid stages were just, with one exception (see below), collected within field margins. This might be indicative of the value of margins as shelter and supply of additional food. Following an insecticide treatment recovery of within-field populations of Coccinellidae may be

mediated via reinvasion from insecticide-free field margins (Hodek & Honěk, 1996); however, to our knowledge no study has been published so far that analysed coccinellid reimmigration into field crops following an insecticide treatment. In previous field studies reinvasion of insecticide treated wheat fields by other predatory groups (Carabidae, Staphylinidae, and Linyphiidae) was shown to take place from untreated sources (Duffield et al., 1996; Holland et al., 2000; Lee et al., 2001). In the current work, sweep net captures indicated that reimmigration of coccinellids into wheat fields began in late July (approximately four weeks post application), presumably mediated by the sharp increase in aphid densities (Hodek & Honěk, 1996; Agarwala & Bardhanroy, 1999). Coccinellid densities were higher, though statistically insignificant, at 4 m than at 24 m distance to field margins, possibly indicating the movement of coccinellids from field margin strips into the crop. However, immigration from other habitats by long-distance flights may also have occurred (Hodek & Honěk, 1996). Within-field, first post-treatment catches of coccinellid larvae were made in late July (i.e. 4.5 weeks p.a.) up to 24 m into the wheat. Under the given field conditions (18°C average temperature, 70 % average humidity) the egg development period for the most frequently captured species *C. septempunctata* and *P. quatuordecimpunctata* was approximately six to ten days (Hodek & Honěk, 1996; Triltsch, 1997; Xia, 1999); therefore the presence of larvae at the end of July indicated coccinellid oviposition activity approximately at the same time as aphid densities peaked (i.e. mid July, four weeks post-application). An oviposition response of coccinellids to high aphid densities has been previously reported (Hodek & Honěk, 1996; Osawa, 2000). Results indicated that the availability of aphid prey is an important pre-requisite for the reimmigration of insecticide treated crops by coccinellids. In 2002 there was no aphid population resurgence, which may be one reason for the low within-field abundance of coccinellids after spraying. However, pre-application samples indicated that densities of coccinellids were generally very low in 2002. This is confirmed by field observations in wheat fields 150 and 250 km, respectively, east of the current experimental site in 2002 (Freier, personal communication).

3.4.11 Reasons for the weak detection of drift effects on populations of beneficial arthropods

Although drift deposit measurement proved the contamination of field margin strips by insecticide drift up to a distance of 3 m from the field edge, few significant effects of λ-cyhalothrin drift on arthropod populations within field margins were detected throughout this study. This was attributed to several reasons. Firstly, λ-cyhalothrin posed a low risk to some non-target arthropods under investigation (e.g. chrysopids, aphid mummies). Secondly, treatment effects were masked by rapid population recovery through sudden immigration of specimens from unsprayed sources (as hypothesised for syrphid flies and aphid parasitoids). Thirdly, population densities of most groups and species of non-target arthropods were too low for statistical analysis. Therefore it was not possible to analyse effects on all groups and species that were collected and counted on the experimental fields. The last point may be of greatest consequence for field studies on the effects of insecticides on non-target arthropods. Field populations of most species or groups captured or counted in field studies are often very low (Moreby et al., 2001; Freier et al., 2002; Kühne et al., 2002). If sample sizes of arthropods are too small, statistical tests will lack power and just few differences between abundances in insecticide treated field plots and controls will be detected (Smart et al., 1989; Moreby et al., 2001; Freier et al., 2002; Studebaker et al., 2003). Therefore, as done in the current study, statistical analysis is often restricted to the estimation of functional group or family level effects. This will inevitably lead to a loss of information because treatment effects on sensitive but less abundant species will remain undetected. These dilemmas may demonstrate the need for an optimisation of sampling methods by adjusting them to the biology (e.g. diel activity, feeding habits, mobility) of organisms under investigation. At the moment, the insufficient knowledge of the ecology of the majority of “indifferent” arthropod species (Büchs, 2003) is the limiting factor of this approach.

4. *Initial dispersal of the aphid parasitoid* Aphidius colemani *Viereck (Hymenoptera: Braconidae) in the field monitored by trap plants**

4.1 INTRODUCTION

Knowledge of the mobility and dispersal of aphid parasitoids is essential for understanding the recolonisation processes into fields after an insecticide application from untreated surroundings. Depending on the active ingredient, insecticide applications in a field crop can lead to an initial depletion of parasitoid and aphid populations (e.g. Holland et al., 2000). Once toxic effects decrease, parasitoid populations within the field (along with their aphid hosts) are likely to recover again. The reinvasion of treated areas may take place from two different sources of parasitoid populations. First, the source of recovery might be located within treated fields, i.e. parasitoids that emerge from the aphid mummy stage, which offers protection against certain pesticides (e.g. Jansen, 1996). Second, parasitoids originate from populations in adjacent untreated off-crop habitats like field margins, fallows etc.. After the application of deltamethrin in wheat Longley et al. (1997a) found a spatial pattern of recovery of aphid parasitoids, which progressed from the edge to the centre. This indicated a reinvasion of parasitoids from untreated surroundings, whereas the recovery of their aphid hosts occurred in a patchy manner. However, Holland et al. (2000) found that dimethoate from treated wheat fields caused a significant decline in parasitoid abundance (*Aphidius* spp.); parasitoids and their hosts took over 20 days to recover although an unsprayed 6 m wide buffer zone was left around half the edge of the field. Until now, it is still unclear whether parasitoids within off-crop habitats actually contribute to a reinvasion of field crops after an insecticide application or if they remain in their habitats and avoid travelling, e.g. in order to minimise travel mortality risks (Weisser & Völkl, 1997; Schwörer & Völkl, 2001). The current study is considered to be a first approach to clarify the complex question of reinvasion processes, which are inextricably linked with parasitoid dispersal capacity. Knowledge of parasitoid dispersal behaviour will enable us to assess the distance from field border habitats into the field that parasitoids are able to cover in certain time frames.

A former field experiment, in which the dispersal of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) into field plots following an insecticide application was analysed (Langhof et al., 2003), initiated the current study. Dispersal was estimated on the basis of parasitised aphids. Low numbers of aphids were successfully parasitised by *A. colemani*. This was primarily explained by adverse weather conditions as well as

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a high background parasitism, suggesting interspecific competition between released *A. colemani* and indigenous parasitoid species. Nevertheless, an alternative explanation could be the dispersal capabilities of the parasitoid, which might prefer long distance migration instead of local migration. Thus, a model field experiment was used in the present work to analyse dispersal capabilities of *A. colemani*. In order to keep background parasitism by naturally occurring primary parasitoids and hyperparasitoids low, the study was carried out on already harvested stubble fields. Dispersal of *A. colemani* was determined on the basis of parasitised *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) aphids on kohlrabi trap plants. Using this kind of release-recovery method it was expected to increase the number of recovered *A. colemani* mummies. Additionally, the number of released parasitoids was not reduced by catching or trapping, as it is common practice in most mark-release-recapture studies.

The objectives of this study were to determine (1) the temporal and spatial dispersal of *A. colemani* following their release and (2) their persistence at the experimental sites.

4.2 MATERIAL AND METHODS

4.2.1 Test Insects

Cultures of the aphid *M. persicae* were maintained in a climatic chamber at 23°C, 50 % relative humidity (RH) and a photoperiod of 16:8 h (L:D). Aphids were reared on kohlrabi (*Brassica oleracea* L. var. *gongylodes* 'Spree') as host plant.
A commercial breeder of biological control agents (Sautter & Stepper, Ammerbuch, Germany) supplied the parasitoid *A. colemani*. All specimens were exposed to the host-plant complex (preconditioning) (Grasswitz, 1998) in order to increase the attractiveness of aphid infested kohlrabi plants to *A. colemani*. Therefore parasitoids were transferred to cages with *M. persicae* infested kohlrabi plants for a 24 h period immediately before field release.

4.2.2 Trap plants

Kohlrabi seedlings were produced by a commercial grower (Nötel, Pattensen, Germany) in mid July 2000. The plants were reared separately in pots (12 cm diameter) and stored in the greenhouse.

Three weeks before the start of the field experiment 900 kohlrabi plants were each infested with ten *M. persicae* (different instars). In order to achieve an infestation with approximately 100 aphids per trap plant at the beginning of the field experiment, aphid infestation was adjusted regularly by removing heavily infested leaves or by adding more aphids. Aphid infested plants were covered with transparent micro perforated polyethylene bags and stored in a greenhouse until experimental use.

4.2.3 Site description

The experiment was carried out simultaneously on three field plots near Pattensen, 25 km south of Hannover (Lower Saxony, Germany). This area is characterised by its intensive farming practise due to fertile clay-loess soils. The landscape is flat and structurally “poor”, i.e. large hedges and woodlots are missing (cf. 3.2.1). To keep background parasitism by naturally occurring primary parasitoids and hyperparasitoids low, already harvested, isolated fields were used to analyse dispersal of released *A. colemani*. To protect kohlrabi plants against mammalian herbivores each experimental plot was fenced in with a screen (1 m height, 3 cm mesh width). The arrangement of the experimental fields and the surrounding landscape is outlined in figure 1.

Wind speed and wind direction were recorded with an anemometer (Lambrecht, Göttingen, Germany) that was positioned between replicates one and two. Meteorological data was monitored at a nearby weather station (1 km) at the Ruthe field station of the University of Hannover.

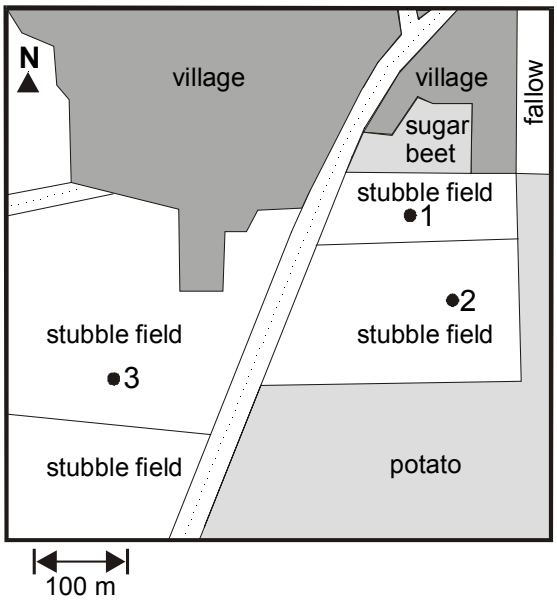

Fig. 1. Outline of the position of the experimental fields and the surrounding landscape. Black circles indicate experimental plots.

4.2.4 Experimental set-up

To estimate parasitoid dispersal aphid infested trap plants were placed equidistantly (2 m interval) on circles (1, 2, 4, 8, and 16 m radius) around the central release point (Fig. 2). On the same day 1,500 adult *A. colemani* (approx. 50 % females, 50 % males) were released at the central release point directly from the rearing cages in which parasitoids got their experience with the host-plant complex. Cages were removed one day later. By that time all parasitoids had left the cages.

The first set of trap plants was replaced with new aphid infested trap plants at day 1 (23 August 2000) the second set of trap plants was replaced at day 3 (25 August) and the third set of trap plants was removed at day 5 (27 August) after the release of *A. colemani*, i.e. the first set of trap plants was exposed for one day in the field and the second and the third set of trap plants was each exposed for two days in the field. Before plants were removed from the field they were visually checked for foraging parasitoids. If parasitoids were detected they were carefully removed to guarantee that they remain in the field and to avoid additional parasitism of aphids. Each plant was covered with a micro perforated polyethylene bag, labelled and stored in the greenhouse to estimate parasitism. One week later each plant was daily inspected for mummies, which were removed with tweezers and kept individually in gelatine capsules in a climatic chamber (20°C, 16 h photoperiod) until adult emergence. This

procedure was repeated over a period of five days. Adult parasitoids were identified according to Starý (1970 & 1973).

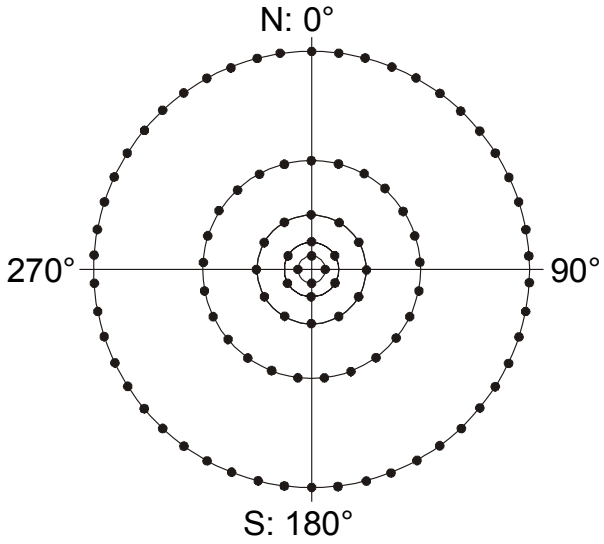

Fig. 2. Arrangement of trap plants around a central release point. Every black spot represents a single aphid infested trap plant; interval between plants is 2 m, radii are 1, 2, 4, 8, and 16 m.

4.2.5 Statistical analysis

Analysis of the dispersal of *A. colemani* from the central release point was done by circular statistics (Batschelet, 1981; Zar, 1999). Each plant with at least one *A. colemani* mummy was counted as a single vector in computing mean vectors for every circle separately. Parasitoid dispersal was characterised by the values r and s. The measure of concentration is given by the value r, which varies from 0 (high amount of dispersion, mean angle of dispersion cannot be described) to 1 (all data are concentrated at the same direction). The mean angular deviation is given by the value s, which ranges from 0° to 81.03°.

Whether there was a mean direction of parasitoid dispersal or whether parasitoids were randomly distributed around the circle was tested by the nonparametric Rayleigh test.

Differences in proportion of trap plants bearing *A. colemani* mummies at different distances from the release point were identified by ANOVA. Where significant F values were obtained ($p < 0.05$), means were discriminated using Tukey's test. The Kruskal-Wallis test followed by Nemenyi-ranking test (Sachs, 2002) was used, if assumptions for parametric tests could not be fulfilled. Percentages were arcsine-transformed. Data analysis was done using the programme SPSS 11.0 (SPSS Inc., 2001).

4.3 RESULTS

4.3.1 Meteorological data

Table 1 summarises weather data recorded during the course of the study. Meteorological data was recorded during the whole experimental period. During the first four hours after the release mean hourly wind speed was 1.5 m/s and mean hourly wind direction 143° (i.e. direction from which wind blows, N = 0°, E = 90°, S = 180°, W = 270°). This period was followed by 14 hours calm. During the second day of the trial average hourly wind direction was 178° (i.e. south), during the third and the fourth day 95° and 98° (i.e. east) and during the fifth and sixth day 267° and 286° (i.e. west). Hourly wind speed over the six days of the trial was light to moderate with a minimum of 0 m/s and a maximum of 4 m/s. Two windless periods were recorded from 22 August (day of the release of the parasitoids) 19.00 h until 23 August 8.00 h, and from 23 August 19.00 h until 24 August 12.00 h. Temperature ranged from 7.0 to 25.5 °C, with an overall mean of 16.1°C. No rainfall was recorded during the experimental period.

Tab. 1. Weather data recorded during the release-recapture trial. Wind direction (i.e. direction wind blowing from): N = 0°, E = 90°, S = 180°, W = 270°.

Date	Hourly wind speed [m/s]			Mean wind direction [°]	Mean temp. [°C]	RH [%]	Rain [mm]
	mean	min.	max.				
22 to 23 August (1st set of trap plants)	0.6	0	1.7	179.2	14.9	68.6	0
23 to 25 August (2nd set of trap plants)	1.6	0	4	107.7	16.0	66.2	0
25 to 27 August (3rd set of trap plants)	1.4	0	4	78.8	18.0	63.9	0

4.3.2 Mummy recovery

In total 593 aphid mummies were collected from trap plants. From these mummies a total of 350 adult *A. colemani* emerged. 71 % of *A. colemani* mummies were detected on plants that were removed on day 1 after release of the parasitoids and 24 % and 5 % of the mummies were collected from trap plants removed on days 3 and 5 after the

release. Numbers of *A. colemani* mummies on trap plants did not differ significantly among the three replicates (Kruskal-Wallis: df = 2, χ^2 = 0.09, p = 0.96). In addition, 204 *Diaeretiella rapae* (M´Intosh), 28 *Praon* spp., nine *Aphidius* spp., and two hyperparasitoids of the genus *Alloxysta* (Alloxystidae) emerged from mummified *M. persicae* removed from trap plants. 44 % of these mummies produced by naturally occurring parasitoids were found on days 1 and 3 after release and 12 % on day 5. Background parasitism of aphids on trap plants did not differ significantly among the three replicates (Kruskal-Wallis: df = 2, χ^2 = 3.58, p = 0.17).

***First day after release of* A. colemani**

On average, *A. colemani* parasitised aphids on 31 % of the trap plants during the first day after parasitoid release (Tab. 2, Fig. 3.1-3.3). A mean number of 3.0 $\pm$ 0.40 SE mummies was detected on each trap plant (Tab. 2). Presence of mummies showed that *A. colemani* moved in each replicate at least a distance of 16 m from the central release point within 24 h after release (Fig. 3.1–3.3). Rayleigh test, small values of r and high values of s indicated that distribution of mummies around the different circles was random (Tab. 3). Only in replicate two at 16 m distance from the release point was the distribution of aphids parasitised by *A. colemani* non-random (z = 3.87, p < 0.05). The distribution of mummies was directed towards southeast (Fig. 3.2), i.e. upwind towards an approximately 75 m distant potato field (Fig. 1). Proportion of trap plants with *A. colemani* mummies were significantly higher on circles at 1 and 2 m distance from the release point compared to the 16 m-distance (Kruskal-Wallis: df = 4, χ^2 = 12.90, p = 0.012). On trap plants with *A. colemani* mummies a mean of 4.9 (1 m), 3.8 (2 m), 1.5 (4 m), 2.5 (8 m), and 2.4 (16 m) mummies were detected per plant. At a distance of 1 and 4 m from the release point numbers of mummies per plant differed significantly (ANOVA: df = 4, F = 3.93, p = 0.036).

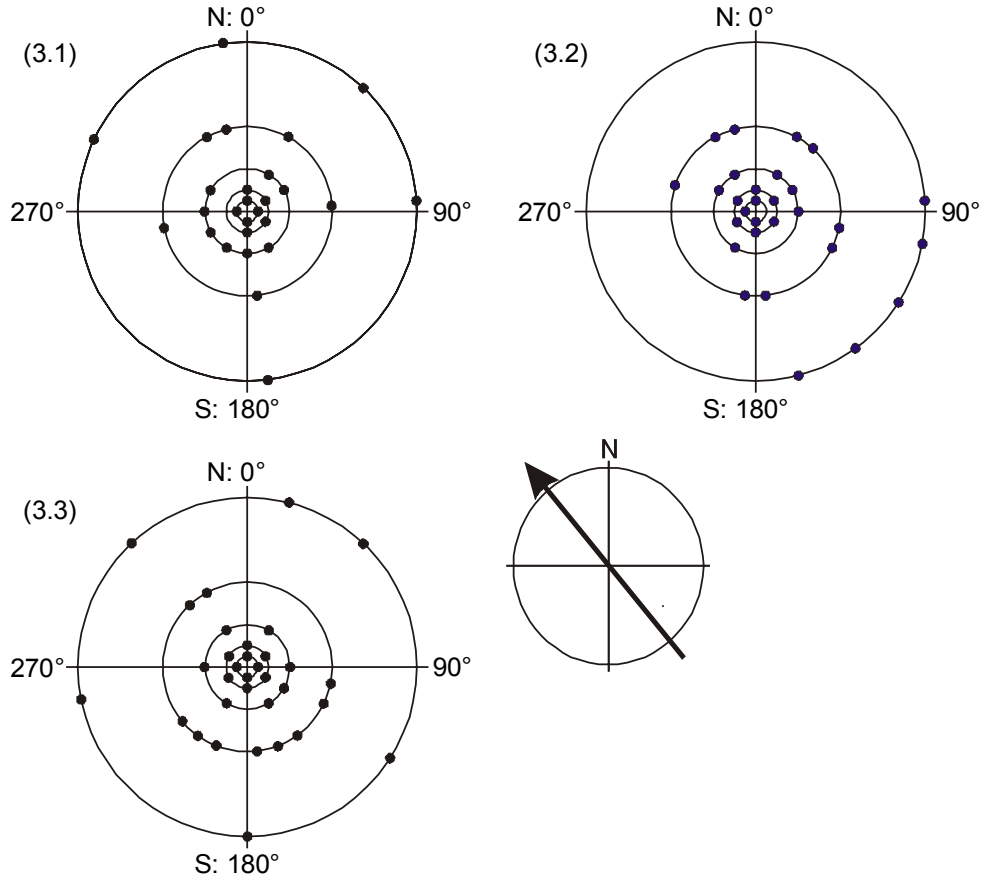

Fig. 3.1 to 3.3. Distribution of trap plants with *A. colemani* mummies at the three experimental plots (1 to 3) one day after release of *A. colemani*. Every black spot represents one trap plant with *A. colemani* mummies; radii are 1, 2, 4, 8, and 16 m. The arrow in the compass card indicates mean wind direction (143°) during the first four hours after release. This period was followed by 14 hours calm.

Tab. 2: Percentage of trap plants with *A. colemani (A. c.*) mummies and mean number of mummies per trap plant 1, 3, and 5 days after release. Different letters in a row indicate significant differences at $p < 0.05$ (% trap plants: ANOVA: df = 2, F = 17.88, p = 0.003, followed by Tukey's test; mummies / plant: Kruskal-Wallis: df = 2, χ^2 = 10.45, p = 0.005, followed by Nemenyi-ranking test.)

	Days after release of *A. colemani*		
	1	3	5
% trap plants with *A. c*. mummies	31 a	15 b	5 c
SE	1.80	4.20	1.60
Mean number of *A. c*. mummies / plant	3.0 a	1.8 ab	1.1 b
SE	0.40	0.29	0.06

Tab. 3: Statistics for the circular distribution of *A. colemani* one day after release. 1, 2, 3: number of replicates as shown in figure 3.1 to 3.3; r: measure of concentration of data; s: mean angular deviation (cf. 4.2.5). Raleigh's z is utilised for testing the null hypothesis of no population mean direction. Asterisks indicate significance ($p < 0.05$).

Replicate	Indices circular statistics	Distance from central release point [m]				
		1	2	4	8	16
1	r	0	0	0.24	0.27	0.29
	s [°]	81.03	81.03	70.57	69.32	68.33
	Rayleigh´s z	0	0	0.47	0.43	0.42
2	r	0.33	0	0.32	0.12	0.88
	s [°]	66.16	81.03	66.72	72.49	28.10
	Rayleigh´s z	0.33	0	0.62	0.36	3.87*
3	r	0	0	0.14	0.41	0.12
	s [°]	81.03	81.03	75.02	62.16	76.07
	Rayleigh´s z	0	0	0.14	1.69	0.08

***Third day after release of* A. colemani**

A. colemani mummies were found in each replicate at all distances from the release point (Fig. 4.1 to 4.3). Proportion of trap plants with *A. colemani* mummies were significantly lower compared to the first day after release but numbers of mummies per trap plant did not differ between the first and the third day after release (Tab. 2). Analysis of circular distributions was carried out although all released *A. colemani* had left the release cage on the first day of the trial, which implies various new starting points from which dispersal recommenced. In some cases data basis was too small for statistical analysis (Tab. 4). Circular distributions showed random dispersal ($r < 0.6$; $s > 51$). Proportion of trap plants with *A. colemani* mummies at different distances from the release point did not differ significantly (ANOVA: $df = 4$, $F = 2.96$, $p = 0.075$). On trap plants with *A. colemani* mummies a mean of 2.2 (1 m), 2.0 (2 m), 1.9 (4 m), 1.9 (8 m), and 1.2 (16 m) mummies were detected per plant. Numbers of mummies per trap plant at different distances from the release point did not differ significantly (Kruskal-Wallis: $df = 4$, $\chi^2 = 3.11$, $p = 0.539$).

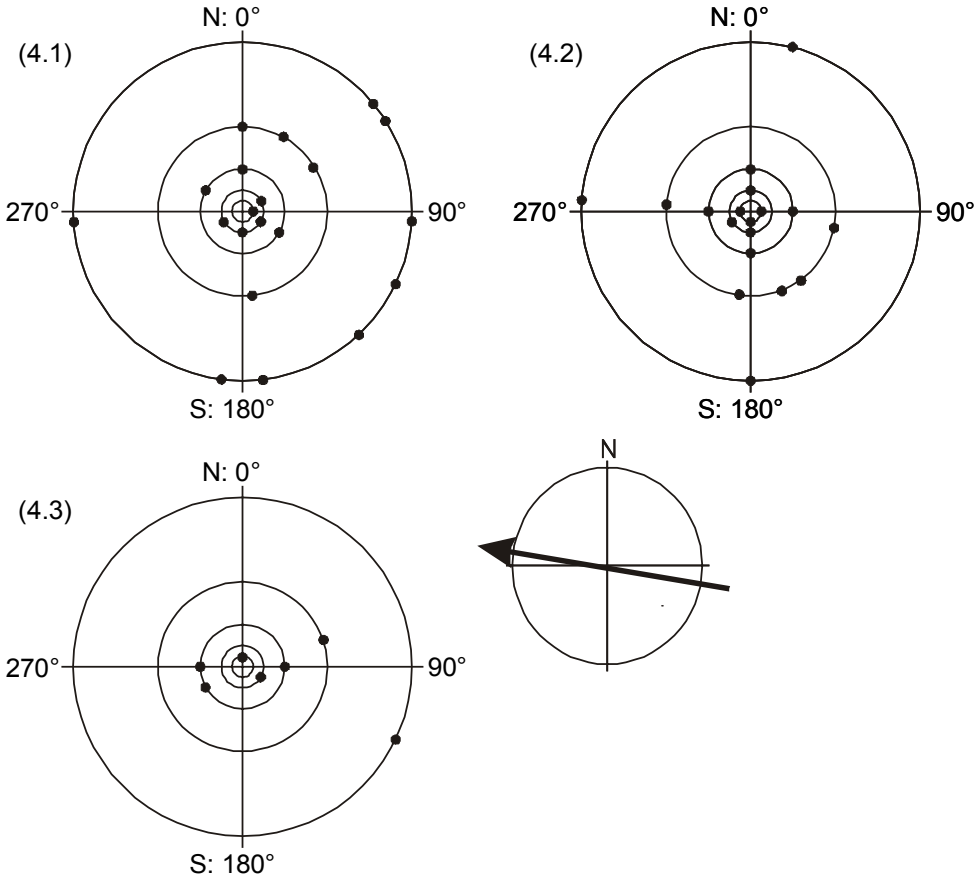

Fig. 4.1 to 4.3. Distribution of trap plants with *A. colemani* mummies at the three experimental plots (1 to 3) three days after release of *A. colemani*. Every black spot represents one trap plant with *A. colemani* mummies; radii are 1, 2, 4, 8, and 16 m. The arrow in the compass card indicates mean wind direction (108°).

Tab. 4: Statistics for the circular distribution of *A. colemani* three days after release. 1, 2, 3: number of replicates as shown in figure 4.1 to 4.3; r: measure of concentration of data; s: mean angular deviation (cf. 4.2.5). Raleigh's z is utilised for testing the null hypothesis of no population mean direction.

Replicate	Indices circular statistics	Distance from central release point [m]				
		1	2	4	8	16
1	r	-	0.43	0.33	0.51	0.49
	s [°]	-	61.01	66.16	56.86	57.95
	Rayleigh´s z	-	0.75	0.33	1.03	1.91
2	r	0.33	0.33	0	0.59	0.25
	s [°]	66.16	66.16	81.03	51.64	70.17
	Rayleigh´s z	0.33	0.33	0	1.76	0.19
3	r	-	-	0.33	-	-
	s [°]	-	-	66.16	-	-
	Rayleigh´s z	-	-	0.33	-	-

***Fifth day after release of* A. colemani**

Five days after the release, *A. colemani* mummies were detected on 5 % of the trap plants. Proportion of trap plants with A. *colemani* mummies were significantly lower than on the first and the third day after release. Numbers of mummies per trap plant were significantly lower compared to the first day after release (Tab. 2). Mummies were found on trap plants at all distances from the release point (Fig. 5.1 to 5.3). On trap plants with *A. colemani* mummies a mean of 1.0 (1 m), 1.0 (2 m), 1.3 (4 m), 1.0 (8 m), and 1.0 (16 m) mummies were detected per plant. Data basis was too small for statistical analysis of circular distribution.

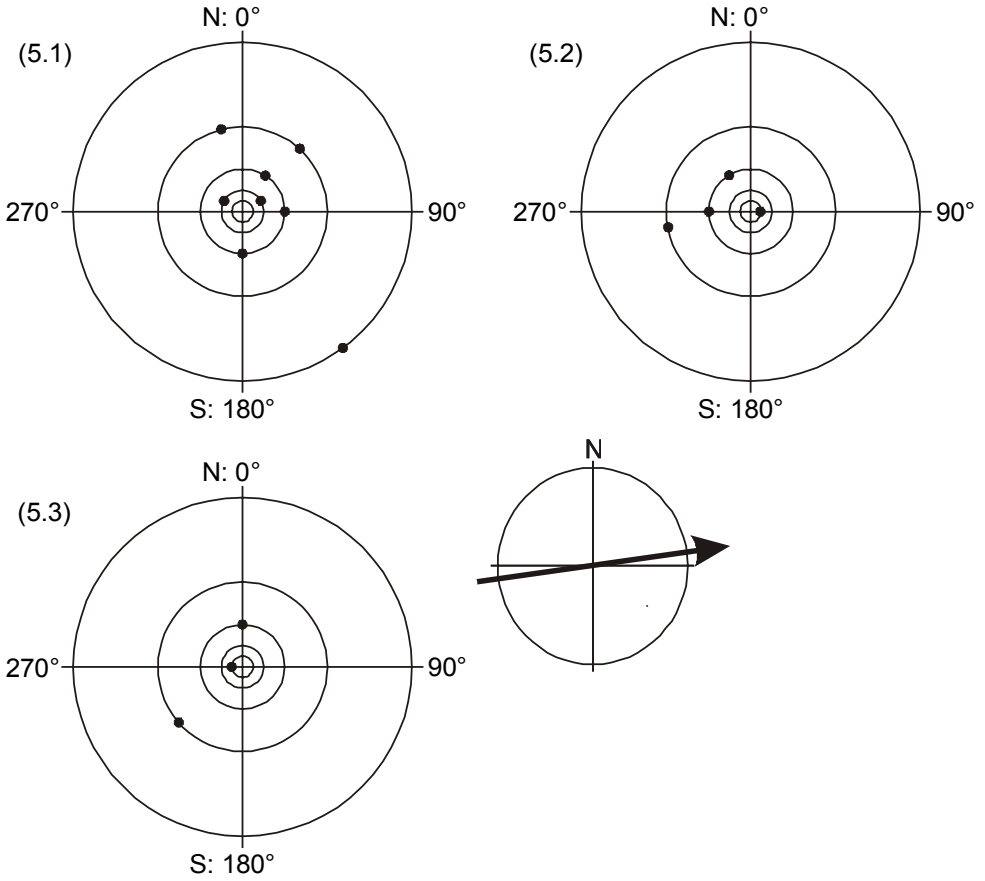

Fig. 5.1 to 5.3. Distribution of trap plants with *A. colemani* mummies at the three experimental plots (1 to 3) five days after release of *A. colemani*. Every black spot represents one trap plant with *A. colemani* mummies; radii are 1, 2, 4, 8, and 16 m. The arrow in the compass card indicates mean wind direction (79°).

4.4 DISCUSSION

4.4.1 *Suitability of the experimental design for dispersal studies with* **A. colemani**

In Europe, *A. colemani* naturally occurs in the Mediterranean area (EPPO, 2001). Additionally, some specimens were found in the Czech Republic (Starý, 2002) and in wheat fields in East-Central Germany (Adisu et al., 2002). However, until now, *A. colemani* seems not to occur naturally in the experimental area; this is indicated by intensive samplings of aphid parasitoids in wheat and off-crop habitats in 2002 and 2003. In addition, it was not found in earlier mummy samplings in Northern Germany (Kiel area) (Petersen, personal communication) as well as in Danish cereal fields (Sigsgaard, 2002). Therefore, it is assumed that all *A. colemani* mummies found in the present study resulted from released *A. colemani*.

The use of a spatially isolated experimental set-up in order to separate aphid infested trap plants from naturally occurring parasitoids and thereby reduce background parasitism was successful. In the current work 59 % of mummies that were collected from trap plants contained offspring of released *A. colemani* and 41 % contained offspring of indigenous species. Compared to the earlier field study (Langhof et al., 2003), where *A. colemani* emerged from only 0.3 % of mummies collected in non-insecticide treated field plots of kohlrabi in July 1999, the proportion of detected parasitoid activity could be increased nearly 200-fold on isolated plots. The structural differences in the environments, in which experiments were conducted, may explain the difference in *A. colemani* recovery between both studies. In the previous field study, releases of *A. colemani* were made at the field station of the University of Hannover in a complex agricultural landscape, which was characterised by small field plots of vegetables, fruit plantations, and small hedgerows. Thus, different aphid species and their associated parasitoids had already been established at the experimental site before *A. colemani* were released. In contrast, the present study was conducted in a simple, non-complex environment with a high proportion of bare land, arable fields of large sizes, and few small landscape elements such as field margins, hedgerows, or woodlots. Trap plants were arranged on stubble fields lacking natural cover. Hence, no alternative aphid species were present at the release site prior to the release of parasitoids. These structural differences in surrounding habitats between both experimental sites are reflected by the higher number of *A. colemani* mummies in the current study.

Nevertheless, a considerable amount of mummies (41 %) was produced by indigenous species, suggesting that even under remote field conditions a total exclusion of naturally occurring parasitoids is almost impossible. The crucifer specialist *D. rapae* was the dominant species (85 %) in background parasitism. The efficient host location behaviour of *D. rapae,* which is known to respond to odours of cabbage plants (Hofsvang & Hågvar, 1991), might contribute to this result. In future field studies on parasitoid dispersal behaviour it might be possible to keep background parasitism much lower by the use of another parasitoid-host-complex.

4.4.2 Dispersal behaviour of released A. colemani

Recolonisation of arable fields by parasitoids from field margin habitats subsequent to insecticide treatments is mainly influenced by the dispersal behaviour of the parasitoids as well as their persistence at the target area. In the present study we assessed both factors on the basis of the temporal and spatial distribution of mummies. Mummy distribution on the first day after parasitoid release allowed an estimation of the initial dispersal of parasitoids, whereas mummy distributions on the third and the fifth day after release reflected the persistence of *A. colemani* at the release sites.

Immediately after their release *A. colemani* had three different behavioural options: First, remaining on the aphid infested release plant, second, short-range dispersal, and third, long distance migration. The first possibility was observed by Weisser & Völkl (1997), who found a majority of released monophagous *Lysiphlebus cardui* (Marshall) (Braconidae) females remaining on an aphid infested release plant; even on aphid free plants parasitoids remained for six days instead of dispersing. Such behaviour was not observed in the current study. The release-cages with aphid infested kohlrabi plants were removed from the fields one day after the release; at that time all parasitoids had left the cages.

In the present work, the short-range dispersal of *A. colemani* was estimated based on the distribution of mummies on trap plants. 4,500 released parasitoids (approximately 2,250 females) produced in total 248 mummies within one day after release. Assuming that each released *A. colemani* female parasitised only a single aphid, at least 11 % of released female parasitoids remained at the release site and successfully parasitised aphids. Mummy pattern showed that *A. colemani* females moved at least a distance of 16 m from the release point within one day after release. Furthermore, mummy density on trap plants indicated that released parasitoids seemed to have spread evenly across the experimental plots within one day. An even distribution was also observed on days

three and five after release. Similar results were obtained by Muratori et al. (2000), who found a homogenous distribution of *Aphidius rhopalosiphi* DeStefani-Perez at distances of 5, 10, 20, and 30 m from a central release point, three days subsequent to their release into a wheat field.

In the present study movement of *A. colemani* was random with regard to the compass direction on the first day after release (with one exception). In several field studies wind was identified to be a major factor influencing the direction of dispersal of minute Hymenoptera (e.g. Schwörer et al., 1999; Marchand & McNeil, 2000; Gu & Dorn, 2001). Nevertheless, wind speed ranging between 2.8 and 4.2 m/s did not affect the dispersal of different *Trichogramma* species (Keller et al., 1985; Smith, 1988; Fournier & Boivin, 2000) as well as a mymarid species (Corbett & Rosenheim, 1996). Because hourly wind speed ranged between 0 and 1.7 m/s (average 0.6 m/s) during the first day after parasitoid release in the present field experiment it is unlikely that wind speed and direction did influence dispersal of *A. colemani*. However, in replicate two at 16 m distance from the release point, a non-random distribution of *A. colemani* mummies was proven. Because replicates were embedded in the same simple landscape and exposed to the same abiotic factors (e.g. wind, temperature) we did not expect to find differences in mummy distribution between the three replicates. In addition, the physiological state of trap plants and aphids as well as numbers of aphids on trap plants was the same at any distance from the release points. Nevertheless, the distribution of *A. colemani* mummies in replicate two was directed upwind towards a potato crop. Reasons for the directed upwind movement of female *A. colemani* might be the attraction of the wasps to visible cues produced by the green background of the closed canopy of the nearby potato field (Fig. 1) or volatile cues from the crop, e.g. produced by aphid-infested plants (e.g. Hofsvang & Hågvar, 1991; Powell et al., 1998). Response of parasitoids to green light has been shown for *Aphidius ervi* Haliday (Goff & Nault, 1984) and *D. rapae* (Vater, 1971). However, in neither of the other two replicates an influence of the adjacent crops (Fig. 1) on the parasitoid distribution was detected. Thus, it is likely that other factors, not determined in this study, contributed to the directed movement of *A. colemani* females in one of the replicates.

Our estimations of females that displayed short-range dispersal indicated that 11 % of released females remained at the experimental plots and parasitised aphids on trap plants. But what happened to the remaining 89 % of released females? Possibly a considerable number of *A. colemani* left the release site immediately after release and dispersed over a larger distance. Messing et al. (1995) reported that after a mass-release of 288,000 *Psyttalia fletcheri* (Silvestri) (Braconidae) 85 % of recaptured females and 67 % of recaptured males were caught on traps higher than the tallest

crop height at a distance of 10 m from the release point. Moreover, scientists reported that co-workers who released the parasitoids visually observed the almost immediate flight of the wasps away from the release area above the crop canopy. Other authors have claimed long-distance dispersal of minute parasitoids after release for augmentative biological control (e.g. Keller et al., 1985; Corbett & Rosenheim, 1996). Concerning the present study, one reason for a migration out of the experimental area might have been the low attractiveness of isolated trap plants to released *A. colemani*. This may have led to an increased flight activity resulting in low parasitism of aphids on trap plants. This hypothesis is supported by laboratory experiments by Schwörer & Völkl (2001), where *A. ervi* females remained significantly longer on an aphid infested plant within a plant canopy than on an isolated aphid infested plant. The authors concluded that parasitoids might display a more efficient foraging behaviour within a dense plant cover because foraging in the presence of a green background may provide the information that potential hosts are nearby. Consequently, the absence of a green background in the present study could have induced an increased flight activity in *A. colemani*.

However, the actual number of released *A. colemani* females that displayed short-range dispersal may have been higher than suggested by mummy densities. Some parasitoids may have stayed in the field without parasitising aphids. Low parasitism of aphids in the field has been reported for *Aphelinus abdominalis* Dalman (Aphelinidae) (Höller & Haardt, 1993). *A. abdominalis* females parasitised four times less aphids in field cages than in the laboratory. The scientists could not explain this unexpected behaviour.

4.4.3 Persistence of A. colemani *at the release site*

The persistence of *A. colemani* at the release site was reflected by the presence of mummies on the third and the fifth day after release. Both proportion of trap plants with *A. colemani* mummies and numbers of mummies per plant significantly decreased with progressing time. Assuming that each released *A. colemani* female parasitised only a single aphid successfully, at least 3.8 % and 0.8 % of the released *A. colemani* females remained at the release site for three and five days, respectively. The decrease in mummy density may have two reasons. First, although the oviposition period of female *A. colemani* continues throughout their whole life span, it decreases with time. In the presence of hosts about 88 % of their eggs are laid within the first two days after emergence (Hofsvang & Hågvar, 1975). However, considering the relatively low

numbers of mummies produced by released *A. colemani* females in our study, despite their high average lifespan fecundity under laboratory conditions (302 eggs at 20 °C) (Van Steenis, 1994), the end of the oviposition period seemed not to be the reason for the decrease in mummy density. But most likely, numbers of *A. colemani* females that survived at the release site decreased with increasing time. Persistence at an experimental area is influenced by mortality, migration of individuals out of the area, and longevity. Under laboratory conditions the average life expectancy of *A. colemani* is 5.8 days (20°C) and 4.4 days (25°C), respectively (Van Steenis, 1994). Thus, under field conditions the majority of the released *A. colemani* was presumably dead at day five after release. In addition, adult parasitoids can be endangered by adverse weather conditions, fungal infections, predation, and parasitism (Brodeur & Rosenheim, 2000). These risks were not quantified in the current study. However, the low number of mummies may also indicate a high natural mortality.

4.4.4 Information provided by the current study concerning the reimmigration into insecticide treated crops by A. colemani

Concerning the recolonisation processes from field margin habitats into insecticide treated fields, results indicate that habitats at a distance of at least 16 m from the field edge can theoretically contribute to a reinvasion by aphid parasitoids. Once they have arrived at different positions within the field, parasitoids may be able to recolonise the crop within a few generations, keeping in mind that the recolonisation of an arable field following an insecticide treatment does not only depend on the ability of an individual parasitoid species to disperse, but also on the persistence of the insecticide previously used in the field as well as the availability of aphid hosts. The tendency of parasitoids to leave their habitat in order to recolonise another habitat cannot be generalised from our data. The results obtained indicate that a certain proportion of parasitoids may not leave their habitats but stay within an area of some square metres throughout their whole lives, whereas others will disperse over longer distances.

The drawback of the current study is that it just provides information on the dispersal of *A. colemani* females but not on the dispersal of males. Therefore, the next step was to track the dispersal of both male and female aphid parasitoids. This was done by mark-release-recapture trials conducted in a complex environment (see following chapter).

5. *Analysing the immigration of the cereal aphid parasitoid* **Aphidius rhopalosiphi** *DeStefani-Perez (Hymenoptera: Braconidae) from field edges into wheat fields, using protein-marking and recapture – does recolonisation of insecticide disturbed wheat fields by aphid parasitoids occur from field margin habitats?*

5.1 INTRODUCTION

After population depletions, e.g. due to insecticide applications reimmigration into fields from field margin habitats by natural enemies of cereal aphids, such as parasitoids and predators, is considered to be one possible way of recovery (e.g. Duffield & Aebischer, 1994; Lee et al., 2001). Several studies found evidence for the recolonisation of insecticide treated wheat fields by carabid beetles from undisturbed surrounding habitats (e.g. Duffield & Aebischer, 1994; Holland & Luff, 2000; Holland et al., 2000) and spiders from within-crop sown weed strips (Lemke, 1999). So far, few studies investigated the potential reimmigration of aphid parasitoids. Results from an earlier study showed that recovery of aphid parasitoids within an insecticide-disturbed wheat field progressed from the edge to the centre (Longley et al., 1997a). Although the source of the parasitoids was not investigated, this spatial pattern of recovery indicated a reinvasion of parasitoids from untreated surroundings. However, the presence of adjacent unsprayed areas does not necessarily entail reinvasion by parasitoids. The application of dimethoate to wheat fields caused a significant decline in parasitoid abundance (*Aphidius* spp.); parasitoids and their hosts did not recover although an unsprayed 6 m wide buffer zone was left around half the edge of the field (Holland et al., 2000).

Lack of data on aphid parasitoid dispersal ability is a major barrier to understanding the reinvasion-mediated recovery of parasitoids following pesticide treatments. Evidence is needed that parasitoids are able to move between habitats, which is a precondition for the recolonisation of crops from surrounding sources (Lavandero et al., 2004). Therefore, as a first approximation, the dispersal of the aphid parasitoid *Aphidius colemani* Viereck was estimated in a replicated model field experiment (cf. previous chapter). The dispersal capability of female parasitoids after point release was assessed on the basis of mummified aphids on trap plants deployed at 1 to 16 m from the release point. Results showed that released *A. colemani* moved at least 16 m within 24 hours following their release. Furthermore, low numbers of mummified aphids on trap plants indicated that the majority of parasitoids might have left the experimental site subsequent to the release. That study was conducted under “artificial” conditions

on freshly harvested fields. In that way it was tried to estimate the dispersal ability of released parasitoids in the absence of conspecifics, hyperparasitoids, or predators that may affect their movement (e.g. Brodeur & Rosenheim, 2000; Petersen et al., 2000). Furthermore the influence of host densities or food sources (e.g. Bruck & Lewis, 1998) on the small-scale (i.e. 16 m) movement of *A. colemani* was maintained constant by the set up of trap plants being equally infested with aphids.

Several field studies have shown the effect of landscape elements on the dispersal of insects. For instance, dense plant stands can act as barriers to the movement of hoverflies (Wratten et al., 2003) or carabid beetles (Frampton et al., 1995). On the other hand, (linear) landscape features can function as corridors along or through which insect movement between habitats is supported (e.g. Dover & Fry, 2001; Tewksbury et al., 2002). Therefore, reliable estimations of the reimmigration capability of aphid parasitoids following insecticide applications require a more realistic experimental approach. Consequently, the next step was to investigate the movement of a local aphid parasitoid species from the field edge into a wheat crop under representative field conditions. Therefore experiments were conducted in a typical agricultural landscape; no manipulations such as adjusting host densities or excluding natural enemies were made.

The dispersal of a species in its natural habitat is typically investigated using mark-release-recapture techniques, which provide the accurate discrimination between the released specimens and their naturally occurring conspecifics (Hagler & Jackson, 2001). In their review article on insect marking methods Hagler & Jackson (2001) described the ideal marker to be persistent, non-toxic to the insect, worker and the environment, easy to apply, clearly to identify, and cheap. Naturally, just those markers should be applied that do not negatively affect the behaviour or fitness of the insects. So far, a number of materials and techniques have been used to mark hymenopteran parasitoids. These techniques include fluorescent dust marking (e.g. Corbett & Rosenheim, 1996; Bellamy & Byrne, 2001; Schellhorn et al., 2004), paint marking (e.g. Desouhant et al., 2003), elemental marking (e.g. Fernandes et al., 1997; Pickett et al., 2004), isotope making (e.g. Prasifka & Heinz, 2004), dye marking (Strand et al., 1990), bacterial marking (e.g. Jackson et al., 2004) and protein marking (Hagler & Jackson, 1998; Hagler et al., 2002b). However, for the current investigations some of these techniques did not come into consideration for marking aphid parasitoids. Due to their small size and the high number of specimens to be marked, the possibility of paint marking aphid parasitoids was rejected. In various studies the effective marking of insects by feeding them a trace element-enriched diet, such as rubidium chloride or caesium chloride (e.g. Qureshi et al., 2004), has been shown. The drawback of using

trace elements is that their detection in insects, which requires an atomic absorption spectrophotometer, is costly and time consuming (Pickett et al., 2004). Recently the protein marking method has been used to effectively mark minute hymenopteran parasitoids (Hagler & Jackson, 1998; Hagler et al., 2002b), virtually without inhibiting their normal behaviour or affecting their longevity (Hagler & Jackson, 1998; Hagler, personal communication). The marker is a commercially available mammalian protein, rabbit immunoglobulin G (IgG), that is suited for either external (by spray) or internal (via ingestion) marking of various insects (Hagler & Jackson, 1998, 2001). The IgG is detected in individual specimens by sandwich enzyme-linked immunosorbent assay (ELISA) using the corresponding specific antibody (anti rabbit-IgG). Due to its approved use, the immunomarking technique was chosen for the current mark-release-recapture studies, designed to investigate the immigration of the aphid parasitoid *Aphidius rhopalosiphi* DeStefani-Perez (Hymenoptera: Braconidae) into wheat fields following their release into the field margin.

This species was selected on account of its importance for the natural control of cereal aphids in Germany and central Europe. *A. rhopalosiphi* was one of the most frequently captured aphid parasitoid species on the three experimental winter wheat fields in the 2002 and 2003 growing season (cf. 3.3.4, page 47). Our findings corroborate previous studies, in which *A. rhopalosiphi* has been shown to be one of the most abundant primary parasitoid species of cereal aphids in Germany (e.g. Borgemeister, 1992; Adisu et al., 2002; Adisu 2003). Due to its frequently high parasitation levels this species is considered to be an important natural antagonist of aphids on cereal crops (e.g. Levie et al., 2000; Sigsgaard, 2002; Langer & Hance, 2004). Therefore, *A. rhopalosiphi* was used in the current mark-release-recapture studies as a model organism in order to investigate aphid parasitoid dispersal from field edge habitats into the crop subsequent to insecticide applications.

The success of a mark-release-recapture study does not only depend on the choice of the right marker but also on the recapture method. Sticky traps and sweep nets are the most commonly used techniques to recapture hymenopteran parasitoids (Hagler et al., 2002a). In the current study, a sweep net (2002), a combination of sweep net and sticky traps (2003) and only sticky traps (2004) were used to recapture IgG-marked *A. rhopalosiphi*. The pros and cons of both recapture techniques are discussed.

The dispersal of small hymenopteran parasitoids is strongly dependent on climatic conditions. In a number of studies it was found that wind (Marchand & McNeil, 2000; Gu & Dorn, 2001), rain (Schwörer & Völkl, 2001) and cloudiness (Vater, 1971; Gu & Dorn, 2001) significantly influence parasitoid performance and movement in the field.

The effects of weather conditions on the outcome of the present mark-release-recapture trials are also discussed in detail.

This study examines (1) the suitability of using rabbit IgG to internally mark the primary aphid parasitoid *A. rhopalosiphi*. In this context, the durability of the IgG in adult parasitoids was determined under greenhouse conditions. (2) The potential of a field margin habitat to act as a source of aphid parasitoids that immigrate into a cereal crop following insecticide applications was assessed. For this purpose several thousands of IgG-marked *A. rhopalosiphi* were released at the field edge of a winter wheat crop. Their ability to migrate into the crop was monitored up to five days subsequent to the release by recaptures at different distances into the wheat. Results of the former dispersal study using *A. colemani* (cf. previous chapter) led to the hypothesis that mass released parasitoids may have displayed long-distance dispersal upon their release into the field. Hence, to evaluate that hypothesis, sticky traps were placed at close distance from the release point at three different heights (ground-level, ear-level, 3 m) to measure initial dispersal of *A. rhopalosiphi*.

5.2 MATERIAL AND METHODS

5.2.1 Test insects

A. rhopalosiphi adults were purchased from a supplier of beneficial arthropods (Katz biotech, Baruth, Germany). Upon arrival parasitoids were stored in a refrigerator (10 °C) for less than 24 hours until used in the experiments. A stock culture of the aphid *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae) had been maintained at the Institute of Plant Diseases and Plant Protection for approximately two years when the current study was initiated. Aphids were reared on winter wheat ('Contur') in wood-framed, mesh-screened cages (60 x 85 x 60 cm deep, self-made) maintained in an environmental chamber at 20°C, 50 % RH with a 16:8 h (L:D) photophase.

5.2.2 Protein-marking A. rhopalosiphi

Adult *A. rhopalosiphi* were internally marked with a mammalian protein, rabbit immunoglobulin G (IgG) (Sigma-Aldrich, Schnelldorf, Germany), by feeding them an IgG-spiked honey solution, as described by Hagler & Jackson (1998).
For the preparation of the marking solution honey ("Maribel Goldklar", Lidl, Neckarsulm, Germany) and bidistilled water (1:1) were added into a 0.6 ml reaction-tube (Biozym, Hessisch Oldendorf, Germany) and stirred using a vortex ("Reax 2000", Heidolph, Schwabach, Germany). After the complete dissolution of the honey, rabbit IgG was added. The mixture was again stirred until complete dissolution. For each trial, fresh marking solution containing 75 mg rabbit IgG per ml honey solution was prepared.
In order to mark large numbers of parasitoids the IgG-spiked honey solution was streaked across the ceiling of an acrylic cage (39 cm heigh x 20 cm wide x 25 cm deep; Savic, Heule, Belgium) using a destroy stick (Biozym, Hessisch Oldendorf, Germany). The sidewalls of the cage were darkened with black plastic film, thereby increasing the tendency of positive phototactic *A. rhopalosiphi* (Starý, 1970) to move towards the marking solution-coated ceiling. Adult *A. rhopalosiphi* were introduced into the cage and maintained in an environmental chamber at 20°C, 60 % RH with a 16:8 h (L:D) photophase for 24 hours.

5.2.3 Identification of immunomarked A. rhopalosiphi *using enzyme linked immuno sorbent assay (ELISA)*

A sandwich ELISA was performed on each parasitoid as described by Hagler & Jackson (1998). The ELISA procedure was conducted as follows:

Coating of wells with specific antibody

- 100 µl goat anti-rabbit-IgG (Sigma-Aldrich, Schnelldorf, Germany) (diluted 1:500 in bidistilled water) were added per well of a 96-well microplate (Greiner, Frickenhausen, Germany)
- incubation at 4°C for 1 h, discarding

Blocking of remaining nonspecific binding sites

- 360 µl non-fat dry milk (diluted 1:100 in bidistilled water) was added to each well
- incubation at 27°C for 30 min., discarding

Incubation with test samples

- each parasitoid homogenized with destroy stick in 150 µl phosphate buffered saline (PBS)
- 150 µl of test sample was added to each well
- incubation overnight at 4°C, discarding

Washing

- wells were washed three times with PBS Tween 20 (0.05 %) and twice with PBS

Incubation with peroxidase-conjugated antibody

- 50 µl of horseradish peroxidase-conjugated antibody (Sigma-Aldrich, Schnelldorf, Germany) (diluted 1:1000 in 1% nonfat milk) was added to each well
- incubation at 27 °C for 1 h

Washing (see above)

Colour development

- 50 µl horseradish peroxidase substrate solution (Bio-Rad, Munich, Germany) was added per well
- incubation at 27 °C for 2 h

Reading of results

- absorbance of each well was measured with a microplate reader (Model 550, Bio-Rad, Munich, Germany) at 405 nm

In each ELISA test, unmarked *A. rhopalosiphi*, which did not come into contact with the IgG, were included as negative controls. To determine a positive ELISA result (i.e. parasitoids that contain rabbit-IgG) Hagler & Jackson (1998) used the mean absorbance value of negative controls plus three standard deviations as cut-off values. However, in the current study this value was very low (< 0.03) and therefore a higher, fixed cut-off value of 0.10 (i.e. visible colour development) was used in order to provide reliable results.

5.2.4 Retention of IgG in A. rhopalosiphi *under "semi-field" conditions*

The marking solution and the cage containing IgG-spiked honey solution were prepared as described above (5.2.2). Additionally, a control-cage was established; this was prepared identically, except that rabbit IgG-free honey solution was used. Approximately 150 adult *A. rhopalosiphi* each were kept within either of the two cages for 24 hours. Both control- and treatment-cage were maintained in an environmental chamber at 20°C, 60 % RH with a 16:8 h (L:D) photophase. After 24 hours, parasitoids were removed from the cages and transferred into two clean cages (one for the marked and unmarked parasitoids, respectively) containing *M. dirhodum* infested wheat plants. To simulate field conditions, these cages were maintained outside under a roof for rain protection. Temperature and humidity were recorded continuously using tinytalk dataloggers (Gemini, Chichester, UK). Beginning with the day after marking (i.e. day 0), 12 marked *A. rhopalosiphi* as well as 12 unmarked parasitoids (i.e. negative controls) were daily removed from the cages using an aspirator. These were individually transferred into 0.6 ml reaction-tubes, frozen (-80°C), and later assayed by ELISA as described above (5.2.3). This procedure was repeated until all parasitoids within the cages died.

5.2.5 Mark-release-recapture trials

In all trials, the marking solution and the cage containing IgG-spiked honey solution were prepared as described above (5.2.2). In 2002 and 2003 mark-release-recapture trials were conducted at field 3, the largest of the three experimental wheat fields (cf. page 39). In 2004 another wheat field was used (see below).

Mark-release-recapture 2002

In 2002 batches of approximately 1,000 IgG-marked *A. rhopalosiphi* were released on 22 June (i.e. six days after the insecticide application to the wheat) at the centre of the weed strip of field 3 at six intervals of 15 m each (i.e. total release of 6,000 parasitoids) (Fig. 1). Recaptures were done at days one, two, three and five after the release by taking four 50-sweep samples along linear transects at 3, 6, 9, 12, 24, and 48 m into the wheat (Fig. 1). At all recapture dates, sweep samples were taken between 9 a.m. to 11 a.m.. The total distance traversed in taking four 50-sweep samples was about 200 m. In the laboratory each captured *Aphidius* spp. was sexed and individually transferred into a 0.6 ml reaction-tube, frozen (-80°C) and later assayed as described above (5.2.3).

In order to ensure the successful marking of released parasitoids, 30 *A. rhopalosiphi* were removed from the release cage immediately prior to release for the detection of the IgG.

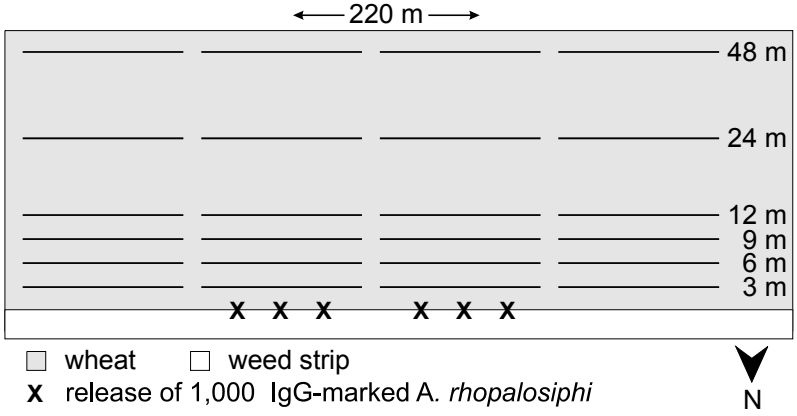

Fig. 1. Schematic graph of the area of the 12-ha wheat field used for the mark-release-recapture experiment in 2002. Lines symbolise transects of 50-sweep samples.

Statistics

The nonparametric Kruskal-Wallis test was used to test whether there were significant differences in numbers of unmarked *Aphidius* spp. captured at different distances from the field edge.

The relationship between the number of *Aphidius* spp. captured during six sweep sampling dates between 20 June and 28 June 2002 and the wind speed while sampling was analysed using nonparametric bivariate correlation. Spearman's rank correlation coefficient, r_s, was computed, which is a measure of the correlation of both test variables.

Differences in numbers of *Aphidius* spp. captured during different wind regimes were elucidated by nonparametric Anova-type statistic (ATS) (Brunner & Munzel, 2002). Using Bonferroni correction, the alpha level (0.05) was adjusted to 0.0031 to compensate for multiple comparisons.
Data analysis was done using the programme SAS version 8.02 (SAS, 2001) and SPSS version 12.0.1 (SPSS, 2004), respectively.

Mark-release-recapture 2003

In 2003 approximately 6,000 IgG-marked *A. rhopalosiphi* were released on 3 July (i.e. 13 days after the insecticide application to the wheat) at a single central release point at the centre of the weed strip of field 3 (Fig. 2). Recaptures were done at days one, two, and three after the release by taking four 50-sweep samples along linear transects at 1, 3, 5, 7, 11, 13, 24, 26, 48, and 50 m into the wheat, as well as within the weed strip at 1 and 2 m from the field edge (Fig. 2). All sweep samples were taken between 9 a.m. to 11 a.m.. The total distance traversed in taking four 50-sweep samples was about 200 m. In addition, to analyse the initial direction of dispersal of *A. rhopalosiphi* upon release, marked parasitoids were recaptured on transparent sticky traps (20 cm wide x 25 cm high, made of clear plastic pockets, Esselte, Stuttgart, Germany), coated on the side facing the release-cage with insect glue (Temmen, Hattersheim, Germany). Transparent traps were used in order to minimise attraction and to capture parasitoids that are actively foraging/dispersing within the crop (Longley et al., 1997a). One sticky trap each was attached vertically to a cane at ground-level, ear-height (approximately 80 cm) and 3 m, i.e. effective trapping was at 0 to 25 cm above ground-level (by traps placed at ground-level), approximately -5 to 20 cm above canopy height (by traps placed at ear-height) and 220 to 245 cm above canopy height (by traps placed at 3 m above ground-level). One cane each was placed at each of the four compass directions (i.e. N, E, S, W) at 2 m distance from the release point (Fig. 2). Six hours after the release traps were removed from the field. Every single captured *Aphidius* spp. was sexed and assayed as described above (5.2.3).
In order to estimate the retention of the IgG in released *A. rhopalosiphi* under the given field conditions, 40 marked A*. rhopalosiphi* were transferred into an acrylic cage with aphid infested wheat plants and placed in the weed strip. Each day eight specimens were removed from the cage for the detection of the IgG.

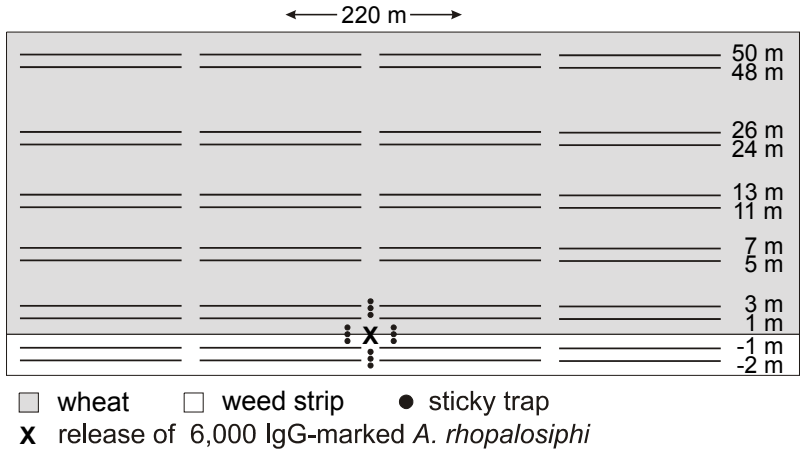

Fig. 2. Schematic graph of the area of the 12-ha wheat field used for the mark-release-recapture experiment in 2003. Lines symbolise transects of 50-sweep samples and dots the arrangement of sticky traps for the initial recapture at different canopy heights.

Mark-release-recapture 2004

In 2004 the release-recapture study was conducted at a different winter wheat field, which was located approximately 1 km south of field 3. The part of the field used for the release-recapture experiment had not been treated with insecticides prior to the release. Due to parasitoid rearing problems, the supplier was just able to provide 5,000 *A. rhopalosiphi* (instead of the desired amount of 10,000). After 24 hours of feeding on the IgG-spiked honey solution, marked *A. rhopalosiphi* were released on 8 July at a central release point at the field edge bordered by an approximately 2 m broad grassy field margin and a dense hedge (3 m broad, > 4 m high). Marked *A. rhopalosiphi* were recaptured on sticky traps (see above), coated on both sides with insect glue, which were positioned on canes just at crop canopy height. This position was chosen since it corresponded to the preferred feeding site of parasitoids´ aphid hosts. The majority of cereal aphids were found to feed on upper parts of the tillers (i.e. *S. avenae* and *R. padi* at ear and flag leaf, *M. dirhodum* at flag, first and second leaf), thereby supposably attracting parasitoids to upper plant areas (Bruck & Lewis, 1998). Forty-five traps were deployed in a 14 x 24 m grid, as shown in figure 3. Sticky traps were replaced with fresh ones at days 1 and 2 after the release, with the third set of traps being collected at day 3 after the release. Additionally, just as in 2003, marked parasitoids were recaptured on 12 sticky traps attached to canes at ground-level, 80 cm and 3 m, which were placed at each of the four compass directions (i.e. N, E, S, W) at a distance of 2 m from the central release point (Fig. 3). These traps were

collected 24 hours after the release and were not replaced by fresh ones. All captured *Aphidius* spp. were assayed as described above (5.2.3).

In 2004 only sticky traps were used for the recapture of IgG-marked parasitoids since it was thought to increase the amount of recapture by the use of a sampling method that is relatively unsusceptible to adverse weather conditions. Furthermore, sticky traps capture specimens continuously (e.g. for 24 hours), whereas sweep netting represents a moment in time.

In order to determine the success of marking, 30 *A. rhopalosiphi* were removed from the release cage immediately prior to release for the detection of the IgG.

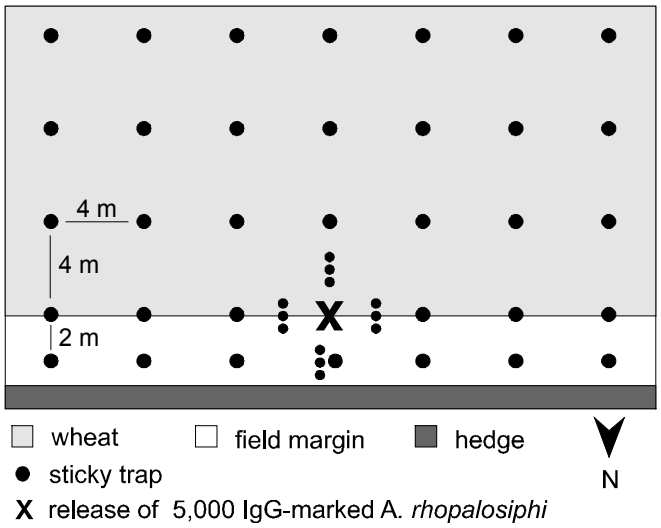

Fig. 3. Schematic graph of the area of the wheat field used for the mark-release-recapture experiment in 2004. ⋮ sticky traps for the initial recapture of *A. rhopalosiphi*, 2 m distant from the central release point at ground-level, ear-height and 3 m.

5.2.6 Weather data

Wind speed and wind direction during the mark-release-recapture trials were recorded at 2 m height at the experimental site using a stationary anemometer (Lambrecht, Göttingen, Germany). Data on temperature, humidity, and precipitation were retrieved from a nearby (1 km) weather station at the Ruthe field station of the University of Hannover.

5.3 RESULTS

5.3.1 Negative controls

All unmarked *A. rhopalosiphi* used as negative controls yielded very low ELISA absorbance values (mean 0.0007 ± 0.015 SD). The low negative control values demonstrated that unmarked parasitoids did not contain rabbit IgG and that there was no cross-contamination between positive and negative samples while conducting the ELISA.

5.3.2 Retention of IgG in **A. rhopalosiphi** *under "semi-field" conditions*

Figure 4 shows the amount of IgG retained in individual *A. rhopalosiphi* on days 1 to 5 after marking in relation to the initial amount contained in parasitoids that were removed from cages at day 0, i.e. subsequent to the 24 hours of exposure to the IgG-spiked honey solution. Although the amount of IgG retained in adult parasitoids decreased over time (Fig. 4), individual specimens contained the immunomarker in sufficient amounts for a positive immunoreaction up to five days after marking. Each *A. rhopalosiphi* removed from cages on day 0 and 1, respectively, showed a positive immunoreaction, as well as most parasitoids (92 %) removed on days 2 to 4. On day 5, 71 % of wasps retained sufficient amounts of IgG for a positive immunoreaction (Fig. 4). These positive immunoreactions showed that most *A. rhopalosiphi* that were held for 24 hours within the cage with an IgG-coated ceiling ingested the IgG-spiked honey solution (Fig. 4). On day 6 both marked and unmarked parasitoids within cages were dead.

Throughout the experiment mean temperature and mean humidity recorded within the cages were 17°C (minimum 12.1°C, maximum 24.3°C) and 73 % RH (minimum 41 %, maximum 96 %), respectively.

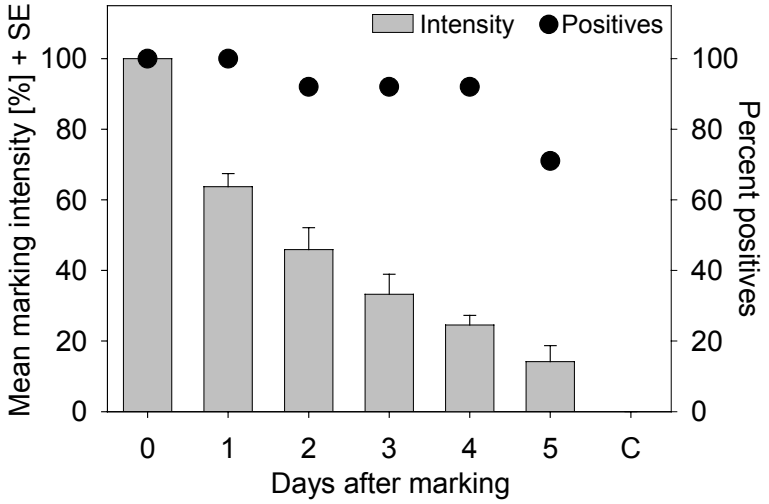

Fig. 4. Retention of rabbit IgG in *A. rhopalosiphi*. The figure shows the marking intensity (+ SE) of parasitoids removed from the marking cage on days 1 to 5 expressed as percentage of the initial amount (i.e. 100 %) of IgG retained in parasitoids removed on day 0 (left y-axis) and the percentage of *A. rhopalosiphi* showing a positive immunoreaction for the presence of the IgG (right y-axis). C = unmarked controls.

5.3.3 Mark-release-recapture study 2002

Weather data

Table 1 summarises the data on wind speed and direction, temperature, relative humidity, and precipitation that were recorded during the course of the mark-release-recapture study in 2002. During the study average hourly wind direction did not vary by more than 36°; south wind blew towards the field margin strip. Mean hourly wind speeds over the five days of the trial were slow (≤ 1.1 m/s) with a minimum of 0 m/s and a maximum of 4 m/s. Mean temperature ranged from 14.4 to 19.1 C° and relative humidity from 75.1 % to 79.1 %. Except for a small amount of rain (0.2 mm) that fell within the first 24 hours after the release, no rain was recorded throughout the trial. Sunshine totalled 42 % (22.6.), 45 % (23.6.), 65 % (24.6.), 47 % (25.6.), 60 % (26.6.), and 29 % (27.6.) of the possible sunshine hours.

Tab. 1. Weather data recorded during the mark-release-recapture trial in 2002. Wind direction (i.e. direction wind blowing from): N = 0°, E = 90°, S = 180°, W = 270°.

Day after release	Recording period	Mean wind direction [°]	Hourly wind speed [m/s] mean	min.	max.	Mean temp. [°C]	RH [%]	Rain [mm]
1	22.6. 13.30 h - 23.6. 12.00 h (1st recapture)	188	1.1	0	3.3	19.1	79.1	0.2
2	23.6. 12.00 h - 24.6. 12.00 h (2nd recapture)	204	1.1	0	4.0	15.6	75.1	0
3	24.6. 12.00 h - 25.6. 12.00 h (3rd recapture)	216	1.0	0	3.5	14.4	75.2	0
4	25.6. 12.00 h - 26.6. 12.00 h (no recapture)	188	0.6	0	2.5	15.7	76.1	0
5	26.6. 12.00 h - 27.6. 12.00 h (4th recapture)	180	1.4	0	4.0	16.9	75.9	0

Effectiveness of marking

All *A. rhopalosiphi* removed from the release cage prior to the release showed a positive ELISA response for the presence of the IgG-marker.

Recapture pattern 2002

A total of 17 (8 males, 9 females) IgG-marked *A. rhopalosiphi* were recaptured during the four sampling occasions. Additionally, 838 *Aphidius* spp. were captured. There were no significant differences in the numbers of unmarked *Aphidius* spp. among the distances on the first, second, and third day of recapture (Kruskal-Wallis: (23.6.) df = 5, $\chi^2 = 5.84$, p = 0.32; (24.6.) df = 5, $\chi^2 = 4.32$, p = 0.51; (25.6.) df = 5, $\chi^2 = 5.64$, p = 0.34). On 27 June significantly more *Aphidius* spp. were captured at 9 m distance from the field edge than at 24 and 48 m, respectively (Kruskal-Wallis: df = 5, $\chi^2 = 15.67$, $p < 0.01$, followed by Nemenyi rank test). For further information on the population dynamics of cereal aphid parasitoids at different distances from the field edge after the insecticide application, refer to 3.3.6. (page 62 et seqq.).

Seven IgG-marked *A. rhopalosiphi* were recaptured on day 1, nine on day 2, none on day 3, and one on day 5 after release (Fig. 5). One day subsequent to the release marked *A. rhopalosiphi* were recaptured up to 24 m into the wheat and on day 2 up to a distance of 48 m into the wheat (Fig. 5).

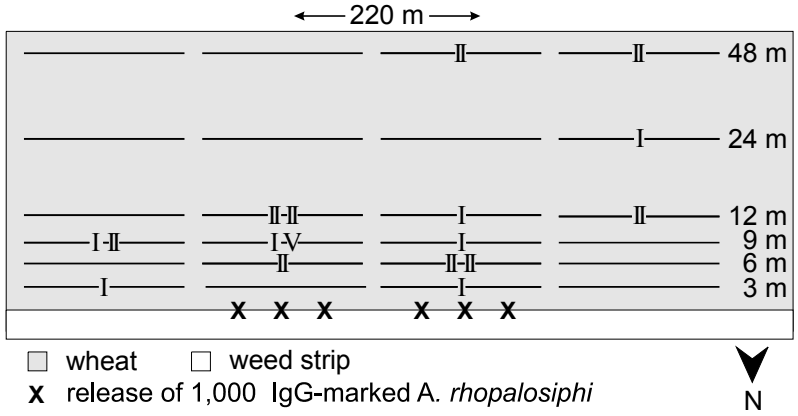

Fig. 5. Recapture pattern in 2002. Each Roman numeral indicates the recapture of one immunomarked *A. rhopalosiphi* by sweep sampling on days 1 (I), 2 (II) and 5 (V) after the release.

Effect of wind speed on capture of* Aphidius *spp. in 2002

Figure 6 shows the mean number of *Aphidius* spp. captured per 50 sweeps and the mean hourly wind speed while sweep netting. Data from the mark-release-recapture trial are supplemented with data of sweep samples taken during the weekly monitoring of parasitoids and leaf dwelling predators at the same sample positions (cf. 3.2.2, page 40 et seq.). Nonparametric correlation proved the significant negative relationship between wind speed and numbers of *Aphidius* spp. captured (N = 108, r_s = -0.727, p < 0.001). During low wind speeds (≤ 1.5 m/s) significantly more *Aphidius* spp. were captured compared with capture periods during which wind speed was higher (> 2.5 m/s) (Fig. 6).

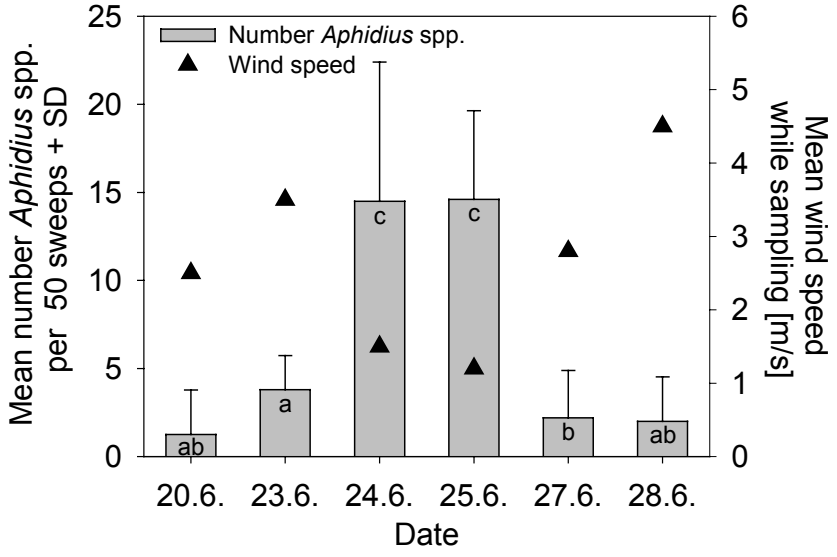

Fig. 6. Effect of wind speed on capture of *Aphidius* spp. using a sweep net. Different letters indicate significant differences (Bonferroni corrected p < 0.0031) between numbers of *Aphidius* spp. captured. Results ATS: df = 102; F = 42.86; p < 0.001.

5.3.4 Mark-release-recapture study 2003

Weather data

During the study wind predominantly blew westerly, i.e. parallel to the weed strip. The wind speed was moderate, with mean hourly wind speeds ranging from 1.6 to 5 m/s. Rainfall was recorded during the first six hours after release (i.e. recapture with sticky traps) and during the next 10 hours until the first recapture with the sweep net. Additionally, rain fell between the second and third recapture (Tab. 2). During the study the sky was mostly covered by clouds, sunshine totalled 32 % (day 0), 0 % (days 1 and 2) and 3 % (day 3) of the possible sunshine hours. Mean temperature ranged from 14.7 to 16.8°C and relative humidity from 76.5 to 83.6 %.

Tab. 2. Weather data recorded during the mark-release-recapture trial in 2003. Wind direction (i.e. direction wind blowing from): N = 0°, E = 90°, S = 180°, W = 270°.

Day after release	Recording period	Mean wind direction [°]	Hourly wind speed [m/s] mean	min.	max.	Mean temp. [°C]	RH [%]	Rain [mm]
0	3.7. 10.00 h - 3.7. 16.00 h (recapture with sticky traps)	254	4.3	3.5	5.0	16.8	76.5	0.8
1	3.7. 16.00 h - 4.7. 12.00 h (1st recapture)	276	3.2	1.6	4.5	15.1	83.6	2.0
2	4.7. 12.00 h - 5.7. 12.00 h (2nd recapture)	285	3.3	2.0	4.0	15.1	82.5	0
3	5.7. 12.00 h - 6.7. 12.00 h (3rd recapture)	311	2.9	2.0	4.0	14.7	83.5	1.2

Retention of IgG in* A. rhopalosiphi *within field cage

All parasitoids that were removed on day 0 and 2, respectively, as well as 88 % of parasitoids removed on day 1 after release from the field cage yielded a positive immunoreaction. On day 1 subsequent to the release 50 % of *A. rhopalosiphi* within the cage were found dead and on day 2 only five living *A. rhopalosiphi* were removed from the cage.

Recapture pattern 2003

During the six hours of initial trapping a total of 65 IgG-marked *A. rhopalosiphi* (35 males, 30 females) were recaptured on sticky traps. Additionally, three unmarked *Aphidius* spp. were captured on sticky traps. Virtually all IgG-marked *A. rhopalosiphi* were captured on traps placed at ground level (Tab. 3). Traps placed at ear height

captured four marked specimens and no parasitoids were recaptured by traps placed at 3 m height. Traps located south of the release point (i.e. 2 m into the wheat) captured the fewest marked parasitoids, whereas traps located east and west of the release point (i.e. at the borderline between wheat field and weed strip) captured most (Tab. 3 & Fig. 7).

Tab. 3. Movement of *A. rhopalosiphi* at 2 m from the release point in 2003: Number of IgG-marked *A. rhopalosiphi* recaptured by sticky traps over a six hours trapping period.

	Number of IgG-marked *A. rhopalosiphi* captured		
Trap location	Ground-level	Ear-level	3 m
North	11	2	0
East	23	1	0
South	4	0	0
West	23	1	0

Recapture by sweep netting was very low. Just two IgG-marked *A. rhopalosiphi* (one male, one female) were captured. One was recaptured on day 1 close to the release point within the weed strip and one on day 3 at 5 m into the wheat (Fig. 7).

By a total of 7,200 sweeps just 44 *Aphidius* spp. were captured. During sweep sampling mean hourly wind speeds were high (3.1 to 3.9 m/s) and the vegetation was wet.

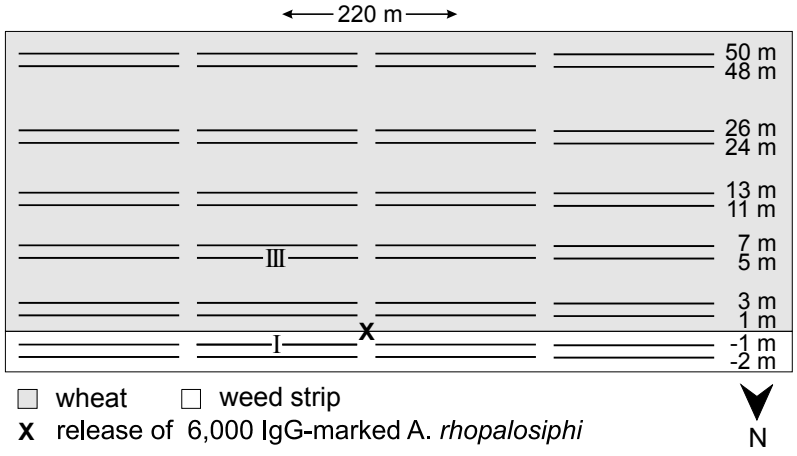

Fig. 7. Recapture pattern in 2003. Each Roman numeral indicates the recapture of one immunomarked *A. rhopalosiphi* by sweep samples taken on day 1 (I) and day 3 (III) after the release.

5.3.5 Mark-release-recapture study 2004

Weather data

During the three days of recapture in 2004 the mean hourly wind speed was too slow (≤ 0.2 m/s) to allow the determination of the wind direction. Two and three days after the release, no wind speed was measured at all. Mean temperature ranged from 13.0 to 17.3°C and relative humidity from 81.7 to 85.0 %. Rainfall was recorded during each of the three trapping periods (Tab. 4), with a maximum of 11.2 mm during the second recapture period. Throughout the course of the study it was partly cloudy/partly sunny, sunshine totalled 4 % (8.7.), 17 % (9.7.), 25 % (10.7.) and 22 % (11.7.) of the possible sunshine hours.

Tab. 4. Weather data recorded during the mark-release-recapture trial in 2004. Mean wind direction not measurable (n.m.).

Day after release	Recording period	Mean wind direction [°]	Hourly wind speed [m/s] mean	min.	max.	Mean temp. [°C]	RH [%]	Rain [mm]
1	8.7. 10.30 h - 9.7. 10.00 h (1st set of sticky traps)	n.m.	0.2	0	0.8	17.3	85.0	1.8
2	9.7. 10.00 h - 10.7. 10.00 h (2nd set of sticky traps)	n.m.	0	0	0	14.9	84.0	11.2
3	10.7. 10.00 h - 11.7. 10.00 h (3rd set of sticky traps)	n.m.	0	0	0	13.0	81.7	1.0

Success of marking

All *A. rhopalosiphi* removed from the release cage prior to the release showed a positive ELISA response for the presence of the IgG.

Recapture pattern 2004

During the first 24 hours of trapping a total of 58 IgG-marked *A. rhopalosiphi* (31 males, 27 females) were recaptured. All of them were captured by sticky traps placed at ground level at 2 m distance from the release point (Tab. 5). 86 % of recaptures were made by traps positioned north of the release point (i.e. at the bottom of the hedge) (Fig. 8); 92 % of these were captured on the side of the trap facing the release point (Tab. 5).

Tab. 5. Movement of *A. rhopalosiphi* at 2 m from the release point in 2004: Number of IgG-marked *A. rhopalosiphi* recaptured by sticky traps over a 24 hours trapping period (cf. Fig. 8). First number in parenthesis: number of trapped IgG-marked *A. rhopalosiphi* on the side of the trap facing the release point; second number in parenthesis: number of IgG-marked *A. rhopalosiphi* trapped on the averted side of the trap.

	Number of IgG-marked *A. rhopalosiphi* captured		
Trap location	Ground-level	Ear-level	3 m
North	50 (46 + 4)	0	0
East	4 (2 +2)	0	0
South	2 (0 + 2)	0	0
West	2 (1 + 1)	0	0

During the subsequent 24 hours of recapture, a total of three IgG-marked parasitoids (one male, two females) were captured. One *A. rhopalosiphi* each was recaptured at 4 m (trap 4), 9 m (trap 12) and 12 m (trap 24) from the central release point (Fig. 8). No recaptures were made during the third day of trapping.

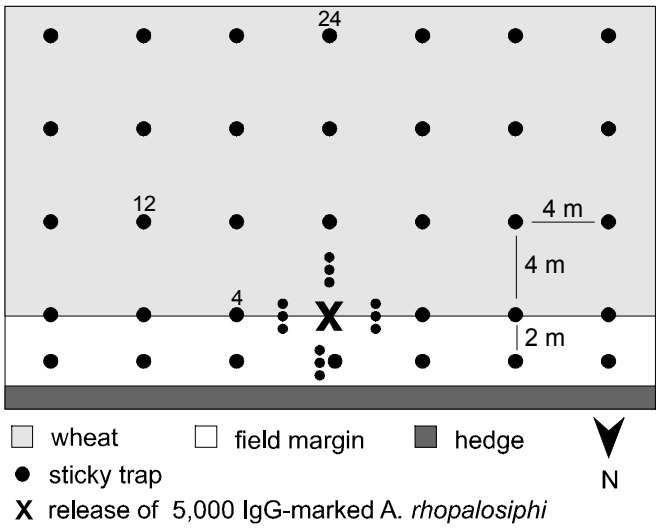

Fig. 8. Recapture pattern in 2004. Sticky traps 4, 12, and 24 each captured one immunomarked *A. rhopalosiphi* on day 2 after the release.

During the three days of trapping in 2004, sticky traps captured a total of 161 (day 1), 26 (day 2), and 19 (day 3) IgG-negative *Aphidius* spp..

5.4 DISCUSSION

5.4.1 Effectiveness of the protein-marking technique

In the current experiments adult *A. rhopalosiphi* were successfully marked with rabbit IgG. All parasitoids that were removed from the marking cages at the end of the marking period showed a positive ELISA response for the presence of the IgG. This result demonstrates that adult *A. rhopalosiphi* fed on the IgG-spiked honey solution. Thereby our findings confirm the results of other experimental studies, in which several hymenopteran parasitoids were successfully marked internally by feeding them an IgG-enriched diet, e.g. *Trichogrammatoidea bactrae* Nagaraja (Trichogrammatidae) (Hagler, 1997), *Anaphes iole* Girault (Mymaridae) (Hagler & Jackson, 1998), *Chelonus curvimaculatus* Cameron (Braconidae), *Encarsia formosa* Gahan, and *Eretmocerus emiratus* Zolnerowich & Rose (Aphelinidae) (Hagler & Jackson, 2001). During the marking period adult *A. rhopalosiphi* were not only observed to feed on the IgG-spiked honey solution, but also to walk on the marking solution-coated ceiling. Therefore, parasitoids possibly were also marked externally via tarsal or antennal contact. This indicates a previous study, where adult *A. iole* were successfully marked by contact with filter paper soaked with a rabbit IgG-solution (Hagler & Jackson, 1998). The parasitoids retained the IgG over their whole lifespan (i.e. eight days). Large amounts of insects have also been marked externally by topical spray. This method has been used for the marking of several insect species (e.g. *Hippodamia convergens* Guérin-Ménenville (Coleoptera: Coccinellidae), *A. iole, Eretmocerus* spp., *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), or *Homalodisca coagulata* (Say) (Homoptera: Cicadellidae) (Hagler & Jackson, 1998; Hagler & Miller, 2002; Hagler et al., 2002b; Blackmer et al., 2004; Hagler, 2004).

ELISA absorbance values of *A. rhopalosiphi* that did not come into contact with rabbit IgG (i.e. negative controls) were very low. Furthermore, none of the negative controls yielded a false-positive result. This is the most important prerequisite for the use of the IgG-marker in mark-release-recapture studies, since these studies require a marking technique that definitely distinguishes marked specimens from their naturally occurring counterparts.

5.4.2 Suitability of the protein-marking technique for mark-release-recapture studies with A. rhopalosiphi

The protein-marking technique was shown to reliably mark adult *A. rhopalosiphi*. The advantage of this marking method is its ease of application; several thousands of parasitoids marked themselves by feeding an IgG-enriched honey solution. The preparation of both the marking solution and the marking cage can be done in less than one hour. Furthermore, in the current investigations no evidence was found that the protein marker affected parasitoid survival, since the adult lifespan did not differ between *A. rhopalosiphi* that fed on IgG-free honey and parasitoids that fed on IgG-spiked honey. Likewise, Hagler & Jackson (1998) did not find indications for a reduced lifespan of immunomarked adult *A. iole*. However, further research is needed to determine whether rabbit IgG causes sublethal effects such as change in the behaviour, mobility, or fecundity in *A. rhopalosiphi*. Laboratory studies are currently underway comparing the behaviour of IgG-marked and unmarked *Eretmocerus* spp. (Hagler, personal communication). Preliminary results indicated that the IgG marker seems not to affect the behaviours of the parasitoids.

However, the labour- and time-intensiveness of the ELISA procedure is a limitation for the use of the protein-marking technique in large-scale mark-release-recapture trials. Particularly when considerable numbers of specimens have to be assayed, as in 2002 when several hundreds of *Aphidius* spp. were captured, alternative marking techniques, such as fluorescent-dust-marking might be more suitable (e.g. Bellamy & Byrne, 2001). The time required to prepare the samples and to perform the ELISA is relatively long (minimum of 5.5 hours incubation time and approximately four hours labour time). In his recent paper Hagler (2004) describes an optimisation of the ELISA that reduces time and work to conduct the assay by approximately 50 %. However, the modified procedure was used to identify externally IgG-marked ladybeetles. Time was saved by not homogenising but just soaking the marked beetles in sample buffer. It may be worth testing whether this improved method can be used for mark-release-recapture studies with aphid parasitoids.

5.4.3 Retention of IgG in A. rhopalosiphi

The present study showed that rabbit IgG can be retained in *A. rhopalosiphi* throughout its adult lifespan. This finding corroborates previous studies, in which the IgG was detected in different adult insects throughout their lifetime (e.g. Hagler & Jackson,

1998; Hagler & Miller, 2002). However, present results indicated that the amount of IgG retained in adult *A. rhopalosiphi* declined over time, resulting in a decreasing percentage of specimens yielding a positive ELISA response with time. Whereas on day 0 and 1 after marking all parasitoids that were fed an IgG-enriched honey solution showed a positive response, the IgG marker was detected in just 92 % of parasitoids on days 2 to 4 and in 71 % on day 5. This result indicates that *A. rhopalosiphi* that are marked internally seem to, although slowly, digest or excrete the protein. Present findings thereby support the results of Hagler & Jackson (1998), who also observed a decrease in the amount of rabbit IgG retained in internally marked *A. iole* over time. So far, no information is available regarding the digestion or excretion mechanisms of the IgG in insects (Hagler, personal communication). However, IgG has been detected in insect frass (Hagler, personal communication).

In the “semi-field” cages adult *A. rhopalosiphi* were supposed to display behavioural activities (e.g. mating, searching for hosts, oviposition) as they would do under field conditions. Therefore it can be assumed that the retention time of IgG by *A. rhopalosiphi* that was observed in the cages might be similar to the retention time in the field.

As a result, the IgG marker can be effectively used for mark-release-recapture studies with *A. rhopalosiphi* since it is detectable in this parasitoid species throughout its adult lifespan. However, further research is required to determine whether rabbit IgG causes sublethal effects to adult *A. rhopalosiphi* (cf. 5.4.2).

5.4.4 Recapture efficiency in mark-release-recapture trials

It is a general problem of mark-release-recapture studies with minute hymenopteran parasitoids that numbers of recaptures are often very low. Although using continuously operating suction traps, Hagler et al. (2002b) recaptured just 0.5 % of released *Eretmocerus spp.*. Using a similar technique, a total of 0.3 % of released *Eretmocerus eremicus* Rose and Zolnerowich were recaptured by Bellamy & Byrne (2001). After mass-release of *Psyttalia fletcheri* Messing et al. (1995) recaptured just 0.3 % of released males and 1.0 % of released females using a grid of sticky traps. In the current study total recaptures of released *A. rhopalosiphi* amounted to 0.28 % (2002) by sweep netting, and 1.12 % (2003) and 1.22 % (2004) by a combination of sweep net captures and sticky traps. Although being low, the recapture success in the present work is therefore in line with previous studies and reflects once more the difficulties arising from the small size of these insects.

However, it is not only the small size of the wasps that accounts for low recaptures, but also the dilemma between the need to enhance recapture (e.g. by the set-up of more traps) and the manpower that is available. An extensive intensification of the recapture effort can also be counterproductive. If traps are set up too densely at close distance from the release point, the majority or released specimens might be captured right upon release (removal trapping).

By sweep netting only 0.28 % (2002) and 0.03 % (2003) of released *A. rhopalosiphi* were recaptured. The almost 10-fold lower recapture in 2003 compared to 2002 was clearly related to the adverse weather conditions throughout the mark-release-recapture study in 2003. Firstly, the wet vegetation and the relatively high wind speeds (3.1 to 3.9 m/s) while sweep netting, hampered the recapture with the sweep net. Secondly, the windy, cloudy and wet conditions most likely greatly reduced the (flight) activity of *A. rhopalosiphi* in the field. Several studies have estimated the effects of weather on the behaviour and activity of hymenopteran parasitoids. A laboratory study on the foraging behaviour of *Aphidius ervi* Haliday indicated that wind (2 m/s) and rain (15 mm/h) can reduce their dispersal activity as well as their inclination to oviposit (Schwörer & Völkl, 2001). Several laboratory studies investigated the effect of wind on the flight behaviour of small parasitic wasps. In wind tunnel experiments male *Aphidius nigripes* Ashmead were unable to fly at wind speeds ≥ 1 m/s; specimens that took off fell immediately to the ground (Marchand & McNeil, 2000). Wind speed of 2 m/s suppressed the flight behaviour of males and females of the aphid hyperparasitoids *Dendrocerus carpenteri* (Curtis) (Megaspilidae) (Schwörer et al., 1999). Specimens of the braconid parasitoid *Diachasmimorpha longicaudata* (Ashmead) did not fly at a wind speed of 0.8 m/s, whereas calm and a low wind speed of 0.4 m/s stimulated their flight activity (Messing et al., 1997). Wind speeds of more than 0.5 m/s greatly reduced the tendency of *Cotesia glomerata* (L.) (Braconidae) to take off and fly (Gu & Dorn, 2001). Several field studies analysed the effect of wind speed and direction on the dispersal of mass released hymenopteran parasitoids. Corbett & Rosenheim (1996) found upwind displacement for *Anagrus epos* Girault (Mymaridae) at wind speeds of less than 4.0 m/s. Keller et al. (1985) reported that upwind displacement of *Trichogramma* spp. (Trichogrammatidae) is not impeded by moderate wind speeds of less than 3.0 m/s and for *Trichogramma minutum* Riley Smith (1988) found a variable directional displacement at wind speeds up to 2.8 m/s. According to Fournier & Boivin (2000) dispersion of *Trichogramma evanescens* Westwood decreased significantly when wind blew above 4.2 m/s for four hours per day, in contrast, dispersion of *Trichogramma pretiosum* Riley was not significantly reduced until wind blew above 4.2 m/s for eight

hours per day. The mark-release-recapture study conducted in 2002 showed that the upwind dispersal of released *A. rhopalosiphi* from the field edge into the wheat was not prohibited by relatively low wind speeds of less than 1.5 m/s. Therefore, this result is in line with the above quoted studies, as well as with the former study on the field dispersal of *A. colemani*. Prevailing light to moderate wind speeds (< 1.5 m/s) did not influence dispersal of released *A. colemani* (cf. 4.3.2, page 120 et seqq.).

By sweep sampling with the 30 cm diameter sweep net it was just possible to catch parasitoids flying close above the crop canopy or foraging on the upper plant parts (i.e. ear, flag, and first leaf). During wind and/or rain small Hymenoptera might hide in protected microhabitats, e.g. in lower strata within the canopy (Corbett & Rosenheim, 1996). Specimens residing in these strata were uncatchable by sweep netting. Low capture success due to adverse weather was also reported by Gu & Dorn (2001). They collected low numbers of *C. glomerata* by sweep netting above canopy height during windy and cloudy conditions. Likewise, wind speed was shown to influence the number of *Aphidius* spp. caught by sweep netting in the current work. In 2002 significantly fewer *Aphidius* spp. were captured at higher wind speeds (> 2.5 m/s) than at lower wind speeds (1.2 and 1.5 m/s), thereby supporting the hypothesis that during windy conditions the majority of wasps may remain in sheltered microhabitats in lower canopy strata. This assumption is confirmed by wind speed measurements at different heights above and within the wheat canopy. Measurements with a small hand held anemometer at 2 m (approximately 1.20 m above crop canopy height), 80 (approximately ear-level), 50, 20, and 10 cm above ground-level showed that wind speed was considerably reduced within the canopy. When wind blew with a speed of up to 6.5 m/s at 2 m height, the vegetation reduced wind speed by more than 60 % at ear-level and by 100 % at 10 to 50 cm.

5.4.5 Initial movement of released A. rhopalosiphi*: recapture pattern at 2 m from the release point*

In 2003 and 2004 sticky traps were placed at 2 m from the central release point at three different heights in order to investigate the initial dispersal of immunomarked *A. rhopalosiphi* right upon their release into the field. In both years these traps captured approximately 1 % of released parasitoids. Almost all recaptured *A. rhopalosiphi* were caught by traps placed at ground-level, few at ear-level (just in 2003) and none at 3 m height.

These recapture patterns confirm the dispersal behaviour of other small hymenopteran parasitoids observed in the laboratory during artificially generated wind and rain (e.g. Messing et al., 1997; Schwörer et al., 1999; Schwörer & Völkl, 2001). As pointed out above (5.4.4), the high mean wind speed of 4.3 m/s measured in 2003 most likely suppressed flights of *A. rhopalosiphi* above wheat canopy height. Recapture pattern suggests that following their release *A. rhopalosiphi* dispersed within the canopy where climatic conditions were more favourable; they seemed not conduct flights above canopy height. Furthermore, the recapture pattern in 2004 indicated that also rain and/or wet foliage can affect the dispersal behaviour of parasitoids. Albeit in 2004 the mark-release-recapture trial was conducted at calm, initial dispersal of released *A. rhopalosiphi* at 2 m from the release point seemed to be concentrated to the lower parts of the canopy. Reduced activity of parasitoids due to rain has previously been reported (Schwörer et al., 1999; Schwörer & Völkl, 2001). Furthermore, cloudiness might have negatively influenced the field performance of released parasitoids. Throughout the recapture period by sticky traps in 2004 the sky was overcasted by clouds most of the time and sunshine totalled just 7 % of the possible sunshine hours. During cloudy conditions the flight activity of *Diaeretiella rapae* (M´Intosh) was reduced and parasitoids remained on plants (Vater, 1971). Similar results were found for the braconid parasitoid *C. glomerata* in wind tunnel studies (Gu & Dorn, 2001).

However, on the second day following the release of *A. rhopalosiphi* sticky traps captured three immunomarked parasitoids at ear-height at up to 24 m into the wheat. It might be suspected that released parasitoids used short periods of more favourable climatic conditions for (dispersal) flights above canopy height. Corbett & Rosenheim (1996) hypothesised similar dispersal characteristics for mass released *A. epos*. They assumed that released parasitoids may have dispersed below canopy height during windy conditions and above canopy height during periods of low wind speed. Aphid parasitoids of the species *Praon abjectum* (Haliday) are reported to disperse above the canopy under favourable weather conditions, whereas under adverse weather conditions they run (Starý, 1970). However, dispersal by running seems not to play an important role in the dispersal of most aphid parasitoids (Vater, 1971). In the current study, recapture pattern on sticky traps placed vertically at the ground showed that released *A. rhopalosiphi* were not trapped while running. Recaptured parasitoids were found all over the trap, providing evidence that most of them were captured while flying at low height (≤ 25 cm) above-ground. In 2003, within the scope of her diploma thesis, Jenny Kraul estimated densities of ground dwelling predators on the experimental wheat fields at different distances from the field edge using pitfall traps. Just few

Aphidius spp. were found in the traps (Kraul, unpublished), corroborating the assumption that aphid parasitoids mainly disperse by flying.

In 2003 most immunomarked *A. rhopalosiphi* were captured by traps placed at 2 m east and at 2 m west from the central release-point, i.e. directly at the borderline between wheat field and field margin. This borderline was characterised by an approximately 20 cm wide gap of bare ground flanked on one side by the wheat and on the other side by the field margin vegetation, thereby forming a kind of alley. Recapture pattern indicated that released parasitoids may have used this borderline as "dispersal corridor". Some previous studies found evidence for the dispersal of insects along linear structures (e.g. Good, 1998; Haddad, 2000; Berggren, 2002; Sciarretta et al., 2003), which can facilitate their movement (Tewksbury et al., 2002). For example, Dover & Fry (2001) showed an increasing rate of movement of three butterfly species along linear wind breaks. Whether *A. rhopalosiphi* tend to disperse along narrow, barrier-free linear structures requires verification through further field based studies. Unfortunately, the release site used in 2004 lacked a distinct borderline between wheat and field edge. Therefore the 2004 trial could not serve as replication of the study conducted in 2003.

In 2004 the majority (86 %) of immunomarked *A. rhopalosiphi* were captured north of the release point by the trap placed at the bottom of the hedge (i.e. away from the wheat crop). This was unexpected, because almost all tillers in the wheat crop were infested by cereal aphids at the time of the release of the parasitoids, therefore aphid infested tillers should have acted as strong stimuli for a directed movement of *A. rhopalosiphi*, although being inexperienced, into the wheat. In laboratory experiments it was shown that naive *A. rhopalosiphi* respond positively to cereal aphid honeydew (Budenberg, 1990). And Poppy et al. (1997) reported a positive response of *A. ervi* to aphid sex pheromones. However, due to the lack of replications, we cannot solve the question whether the movement of released *A. rhopalosiphi* towards the hedge was random or oriented, e.g. due to (undetermined) visual or olfactory stimuli (e.g. Goff & Nault, 1984; Hågvar & Hofsvang, 1991). Furthermore, we do not know whether released parasitoids crossed the hedge and left the experimental site. However, due to its width and density it is suspected that the hedge might have acted as a barrier to the movement of *A. rhopalosiphi*. This assumption is supported by studies on the permeability of landscape features for beneficial insects. Wratten et al. (2003) found a significantly reduced movement of hoverflies through lines of poplar. And the movement of carabid beetles can be negatively affected by dense field boundaries (e.g. Frampton et al., 1995).

5.4.6 Migration of A. rhopalosiphi *from the field edge into the crop: within-field recapture pattern*

In all three study years it was shown that several released *A. rhopalosiphi* moved from the field edge into the wheat. The distance traversed by IgG-marked *A. rhopalosiphi* in the current work agrees with previous reports on the dispersal capability of aphid parasitoids. Following their release into the field, *A. rhopalosiphi* moved at least a distance of 30 m within three days (Muratori et al., 2000) and *A. colemani* females dispersed at least a distance of 16 m within one day (cf. previous chapter). In greenhouse experiments *A. colemani* were able to cover distances of at least 12 m within 6 hours (unpublished own observation) and 45 m within 48 hours (Van Schelt, 1994). Individual *D. rapae* females were observed to perform non-stop flights over a distance of at least 10 m (Vater, 1971). However, since passive dispersal of aphid parasitoids by wind does also occur (Starý, 1970), it can be taken for granted that under certain circumstances individual specimens might disperse much farther than the distances reported in previous studies and the present work.

Temporal and spatial recapture pattern in 2002 may be indicative of a movement into the crop that progressed from the edge to the centre over time. On the first day subsequent to the release all recaptures were made at 3 to 24 m from the field edge, whereas within two days after release immunomarked parasitoids penetrated at least 48 m into the crop. Recapture pattern in 2004 might confirm this hypothesis. Whereas released parasitoids seemed not to have dispersed over long distances within the first 24 hours following their release, four specimens were recaptured on the second day within the wheat, indicating that released *A. rhopalosiphi* were capable of moving at least 24 m from the release point into the crop. Due to the low recapture success in 2003, no firm conclusions can be made concerning the dispersal of released *A. rhopalosiphi*. However, the patterns of immigration observed in 2002 and 2004 may reflect the natural reinvasion of an insecticide treated field by *Aphidius* species from unsprayed surroundings. Some previous studies showed a post-treatment recovery of beneficial invertebrate populations that progressed from the edge to the centre of cereal fields (Duffield & Aebischer, 1994; Duffield et al., 1996; Longley et al., 1997a). Scientists hypothesised that the observed recovery pattern was indicative for a reimmigration into the treated areas from untreated surroundings, which acted as source of potential “colonists”.

The persistence of the insecticidal activity is an important factor determining the recolonisation of insecticide treated fields by (non-target) arthropods. In the current work, mass-releases of immunomarked *A. rhopalosiphi* were made six (2002) and 13

(2003) days following the application of λ-cyhalothrin to the wheat. Although this insecticide is inherently toxic to *A. rhopalosiphi* (Sterk et al., 1999), the toxic effects of λ-cyhalothrin to this parasitoid species are of short duration, i.e. less than 3 days (Jansen, 2001). Laboratory toxicity tests with *A. colemani* support this finding, 24 hours exposure to four-day old λ-cyhalothrin deposits on leaf surfaces resulted in low (< 12 %) corrected mortality of wasps (Fiedler, unpublished). As a result, in the present study the dispersal of released *A. rhopalosiphi* into the wheat was most likely not affected by the previously applied insecticide.

The discussion of the current results primarily focuses on the effect of climatic conditions (e.g. wind, rainfall, and cloudiness) on the dispersal of released *A. rhopalosiphi*. However, parasitoid movement is a very complex process, which is, in addition to climate, influenced by various biotic factors, such as attraction towards particular habitats or food sources (Bruck & Lewis, 1998; Thies & Tscharntke, 1999), travel mortality risks (Weisser & Völkl, 1997; Schwörer & Völkl, 2001), repulsion by hyperparasitoids (Höller et al., 1994; Petersen et al., 2000), predation (Brodeur & Rosenheim, 2000) as well as host availability and distribution (e.g. Starý, 1970). Furthermore dispersal of parasitoids in the field is affected by their physiological condition (i.e. mating status, egg-load, flight fuel, and hunger) (e.g. Bellamy & Byrne, 2001; Woiwod et al., 2001; Desouhant et al., 2003; van Lenteren, 2003). However, within the framework of this study it was not possible to quantify all of these factors possibly influencing the movement of *A. rhopalosiphi* in the field. As a result, additional field studies are needed for a better understanding of the dispersal of aphid parasitoids.

5.4.7 Gender-based dispersal of IgG-marked A. rhopalosiphi

In the present study, recapture pattern of released *A. rhopalosiphi* did not indicate differences in the dispersal behaviour of males and females. However, due to the relatively low recapture the current study can only give limited information on the gender-based dispersal of this species. Some earlier studies found gender-specific flight and dispersal behaviour in hymenopteran parasitoids, e.g. in the whitefly parasitoid *E. eremicus* (Bellamy & Byrne, 2001; Blackmer & Cross, 2001; Hagler et al., 2002b) and in *Trichogramma* species (Martel & Boivin, 2004). In wind tunnel studies significantly more *E. eremicus* females than males conducted directed flights towards a visual plant cue, and more males than females showed the tendency for migratory flights (Blackmer & Cross, 2001). A mark-release-recapture study, however, indicated

the propensity of males to disperse on a local scale (10 m radius), whereas females seemed to have left the area of release immediately, presumably to search for hosts, which were rare at the release site (Bellamy & Byrne, 2001). Gender-based differences in the dispersal of parasitoids were explained by the different needs of males and females. While the flight behaviour of (mated) females is suspected to be driven by the search for hosts, male dispersal might be primarily influenced by the search for mates (Starý, 1971; Marchand & McNeil, 2000). Furthermore, the mating-status affects the dispersal behaviour of hymenopteran parasitoids, for example unmated *E. eremicus* displayed longer flights than mated ones (Bellamy & Byrne, 2001), whereas in the pteromalid *Nasonia vitripennis* (Walker) mating increased the flight duration (King, 1993). Reviewing the gender-related differences in the dispersal behaviour of other hymenopteran parasitoids, differences in the dispersal between male and female *A. rhopalosiphi* might also be expected. So far, no published information on the gender-based field dispersal in *Aphidius* species is available.

5.4.8 Persistence of IgG-marked A. rhopalosiphi at the release-site

As seen in the three mark-release-recapture trials, the persistence of released *A. rhopalosiphi* at the release site seemed to be relatively low. More than 94 % of recaptures were made within the first 48 hours after release. Thereby the results from the present work support those from the study on the dispersal of *A. colemani* (cf. previous chapter). There might be two possible reasons for this short persistence. Firstly, after an initial short-distance dispersal parasitoids displayed long-distance migration. However, given that in all three study years the host-plant-complex was present and should have favoured the residence of released parasitoids in the field (e.g. Hågvar & Hofsvang, 1991) this explanation might be relatively unlikely. Furthermore, in 2003 and 2004 climatic conditions presumably did not support long distance migrations.

Secondly, and most likely, the main recapture over a relatively short period reflected the longevity of released *A. rhopalosiphi* under field conditions. Upon release, parasitoids were at least two days old, thus the majority may have died until the third day after the release. Observations made in 2003 support this assumption. Approximately 50 % of *A. rhopalosiphi* within field cages had died within one day after release and no living specimens were found on day 3 after release. However, whether the relatively short life span of *A. rhopalosiphi* within field cages actually reflected the "normal" longevity of parasitoids under comparable field conditions or if it rather

reflected the quality of *A. rhopalosiphi* purchased from the breeder, cannot be concluded satisfyingly.

5.4.9 Suggestions for increasing recapture in future mark-release-recapture studies

The clear drawback of the current work was the low amount of recaptured IgG-marked *A. rhopalosiphi*. For future studies an increase in recapture numbers is urgently desired to obtain a sufficient database to allow statistical analysis. To enhance the amount of recaptured specimens we suggest several approaches. First, the amount of marked insects that are released should be increased. For example, in mark-release-recapture studies with whitefly parasitoids several ten thousands of marked wasps were released (Bellamy & Byrne, 2001; Hagler et al., 2002b). As a result, although percentage of recapture was low (≤ 0.5 %) actual numbers of caught specimens were high enough for the application of statistics. However, due to its limited commercial availability it might be difficult to obtain *A. rhopalosiphi* in such high numbers, i.e. own rearing of parasitoids might be necessary.

Second, recapture has to be intensified, i.e. by setting up more sticky traps not only in vertical direction within the crop but also in horizontal direction in different canopy strata. The combined use of different sampling methods might also increase the amount of recaptures. However, if applied effectively, the restriction to one trapping method may be sufficient. In 2004 just sticky traps were used for the recapture of *A. rhopalosiphi* due to their advantages over sweep netting under certain circumstances. The stationary sticky traps can be more effective than sweep net captures, since they capture continuously, they can be used during wind and rain, their set-up is relatively non-destructive to the vegetation, and they can easily be positioned at different canopy heights. However, results of the present study definitively showed the need to set up more traps.

Third, mark-release-recapture studies should be conducted under climatic conditions that favour the field performance of the released species. Needless to say, this is the most problematic demand. In the current work the release-date had to be fixed approximately six weeks in advance due to the time needed for the mass-rearing of insects by the commercial breeder. Once having been delivered, the trial had to be started within 24 hours, because the short lifespan of aphid parasitoids under field conditions limited the possibility to wait for optimal weather conditions.

However, although data indicated that individual specimens of released *A. rhopalosiphi* moved from the field edge into the wheat, it does not necessary follow that naturally occurring parasitoids behave identically and show inclination to leave their field margin habitat in order to migrate into the adjacent crop. Furthermore, we do not know what portion of a population is actually involved in dispersal. In future studies, more emphasis might be placed on estimating the spatial population dynamics of naturally occurring parasitoid populations in field margin habitats, e.g. using biochemical genetic markers, pollen markers, or dyes (e.g. Hagler & Jackson, 2001; Wratten et al., 2003; Lavandero et al., 2004; Schellhorn et al., 2004).

6. FINAL DISCUSSION

The intended purpose of this final discussion is to conclusively discuss results of the current work; it shall not be a repetition of the discussions made in previous chapters. Thus, detailed discussions, e.g. on the toxicity of λ-cyhalothrin to indicator organisms or marking techniques for dispersal studies etc., are given in the respective chapters.

6.1 Evaluation of current risk mitigation strategies for insecticide drift

In Germany the application of insecticides on arable land is subjected to buffer zone restrictions to avoid unacceptable risks for adjacent terrestrial (i.e. field margins, hedgerows, woodlots or tree rows) or aquatic habitats (e.g. watercourses, ponds) due to drift (BBA, 2002a; BVL, 2003). The buffer zone is defined as a pesticide-free area of the crop at the field margin (Candolfi et al., 2001). In Germany the use of the insecticide λ-cyhalothrin on arable land bordered by field margin habitats is restricted by the buffer zone restriction NT103 (BVL, 2003; Syngenta, 2004). By definition, the buffer zone has to be 20 m wide when spraying is done using a standard, i.e. non-drift reducing nozzle type, or using low drift nozzles that reduce airborne spray drift by 50 or 75 %. No buffer zone has to be incorporated when low drift nozzles are used that are listed in the 90 % drift reduction class (listed in the official list of drift reducing technique; Rautmann, 2001). These restrictions have not to be considered when the adjacent terrestrial habitat is agriculturally or horticulturally used (or when it is a path, road, or square) or when it is less than 3 m wide. Furthermore, restrictions do not apply to agricultural fields that are situated in regions with “sufficient” proportions of small landscape elements, such as field boundaries, hedges, and woodlots (BBA, 2002b).

In the current investigations non low-drift multirange flat spray nozzles were used, i.e. the insecticide was applied under realistic worst-case conditions. Nevertheless, few significant drift effects on the insect groups under investigation were found. Thus, it is supposed that the recommended buffer zone restrictions and the use of the 90 % drift reducing technique, respectively, might provide an acceptable risk mitigation measure for the protection of a wide range of arthropods in terrestrial off-crop habitats from λ-cyhalothrin drift. Given that the registration of drift reducing nozzles is based on series of spray drift measurements on bare ground using artificial collectors (petri dishes), it is supposed that the extent of drift is much lower when spraying is done under more realistic conditions. This is shown by drift measurements made by Koch et al. (2003). They compared drift deposition on plant surfaces in a meadow with those on petri

dishes on bare ground using three different nozzle types (standard, 50% and 90 % drift reducing nozzles). Overall, deposits on plant surfaces were much lower than those on petri dishes. Furthermore, they did not find significant differences between deposits on plant surfaces produced by 50 % and 90 % drift reducing nozzles, whereas on petri dishes the 90 % drift reducing nozzles produced lower deposits. This difference in drift deposition was explained by the different conditions under which measurements were done (i.e. bare ground vs. meadow). The meadow reduced spray drift by wind speed reduction, drift interception, and dispersion of the spray cloud due to turbulences in the wind produced by the rough surface of the meadow (Miller et al., 2000; Koch et al., 2003). Drift reduction due to the filtering process of a vegetation canopy has also been shown in earlier studies (e.g. Longley & Sotherton, 1997; Longley et al., 1997b; Rautmann et al., 1997). In addition to buffer zones, windbreaks, either natural (e.g. hedges, tree rows) or artificial (e.g. synthetic windscreens), can be used to protect susceptible terrestrial or aquatic habitats (Ucar & Hall, 2001; Brown et al., 2004). However, drift mitigation by windbreaks due to wind speed reduction and filtration of spray droplets depends on the structural parameters of the vegetation, such as its density, width, height, leaf area index, or capture efficiency (Ucar & Hall, 2001). Dense vegetation with low aerodynamic porosity will not allow airstreams to pass through, resulting in a wall effect, i.e. the airflow is led above and over the canopy (Davis et al., 1994; Miller et al., 2000; Ucar & Hall, 2001). Therefore, due to turbulences generated by dense vegetation, spray droplets can be shifted to areas beyond it. This was shown by Davis et al. (1994), who found a sheltered zone with low drift deposition and reduced drift effects on indicator organisms (plants and insects) immediately behind a 1.6 m high and 1.2 m wide hawthorn hedge. This zone was followed by a zone of increasing drift deposition and non-target effects before declining at greater distances from the hedge.

However, deposit measurements by Koch et al. (2003) indicated possible risks for off-crop habitats at 1 m from the field edge, even when using 90 % drift reducing technique. Regardless of nozzle type, variability in deposits on plant surfaces was highest at close distance from the field edge, whereas at farther distances it was lower. This can be explained by peak deposits at 1 m, which are thought to result from fan geometry as well as from horizontal and vertical spray boom movements while spraying, e.g. due to driving over bumpy ground (e.g. Longley et al., 1997b; Koch et al., 2003). Some peak deposits on off-crop plant surfaces at 1 m distance from the field edge were also measured in the current study (cf. 2.3.2, page 14 et seqq.). Whereas in Germany plant protection products must not be applied in the immediate vicinity

(federal state-specific regulations of minimum distances, e.g. 1 m in Lower Saxony) of surface waters (anonymous, 1998/2004), no equivalent restrictions exist for the protection of terrestrial habitats.

Drift reducing nozzles were widely sold in Lower Saxony in the late 1990s; approximately 95 % of newly delivered application devices were equipped with drift reducing nozzles (Ripke & Warnecke-Busch, 1999). However, so far no data on their actual use are available. To date, many (old) field sprayers have not been equipped with low-drift nozzles (Koch, personal communication). Furthermore, drift reducing technique seems not to be widely distributed in some other EU states (e.g. France) (Koch, personal communication).

The farmers´ acceptance of drift reducing technique will doubtlessly depend on the effectiveness of these nozzles to provide adequate pest control. In addition to wind speed and direction, droplet size is the most important factor affecting pesticide drift. Drift-prone droplets are smaller than 100 µm (e.g. Koch & Weißer, 2004). Low-drift nozzles produce a medium to coarse droplet size spectrum, i.e. they increase the droplet size and minimise the amount of small, drift-prone droplets, thereby reducing the extent of drift. While large droplets reduce the amount of drift, there is concern that they might not provide equal spray coverage of foliage with pesticides as achieved with finer droplets. Poor target coverage might negatively affect pest control under certain circumstances, e.g. the control of grass weeds at early growth stage can be less efficient when herbicides are applied with low-drift nozzles (e.g. Wolf, 2000). Insecticides against several apple pests were less effective when applied with drift reducing nozzles compared to standard nozzles (Lesnik et al., 2005). However, some comparative studies on the effectiveness of different nozzles conducted in orchards found contrary results. Knewitz et al. (2002) compared the biological efficacy of pesticides against fungi and arthropod pests in apple orchards using standard and drift reducing nozzles. The nozzle type did not influence the effectiveness of pesticides. Similar results were reported by Frießleben et al. (2003), who also found no effect of nozzle type on the efficacy of fungicides applied in apple orchards. However, it is suspected that results like those obtained by Lesnik et al. (2005) might not encourage farmers to use drift reducing nozzles.

The EU Council Directive 91/414/EEC (EEC, 2004) mandates that plant protection products must not cause unacceptable effects on the environment and on non-target species. For within-crop non-target arthropods Barrett et al. (1994) defined effects as unacceptable if “no recovery occurs within reasonable time (maximum time, e.g. one season)”. Therefore the German Federal Biological Research Centre (BBA) elaborated

a drift risk management system that accounts for local conditions of the agricultural area in which a certain plant protection product is applied. Kühne et al. (2000) concluded that the proportion of small off-field sites at the landscape level in an agricultural area should be considered in the development of buffer zone restrictions, since it is thought that these sites have an important function for the recovery of pesticide depleted arthropod populations both in arable crops and in adjacent drift contaminated habitats. Based on earlier studies (e.g. Bohn et al., 1989; Kaule, 1991) it was concluded that a proportion of 5 to 20 % of small landscape elements would be sufficient to ensure immigration-mediated recovery of pesticide disturbed populations. As a result, buffer zone restrictions for plant protection products do not apply to German districts with "sufficient" proportions of small landscape elements (BBA, 2002b).

However, the drawback of this risk mitigation concept is that it does not account for the quality of the habitat types adjacent to agricultural fields. Therefore, this softening of the restrictions may involve substantial risks for environmentally valuable and sensitive habitats that do not have to be protected from pesticide drift just because the district possesses a certain proportion of small off-field sites.

The second drawback of the buffer zone restrictions is that they do not apply to field margins that are less than 3 m wide. From the point of view of environmental protection this exception is not comprehensible. However, it was decided to incorporate this exception for pragmatical reasons, based on the belief that farmers would destroy existing field margins to avoid buffer zones while applying pesticides (Kühne et al., 2000). Although one would assume that farmers do not act like that, destruction of field margins for these reasons is known to happen (Koch, personal communication). In this case it seems to be better to abandon buffer zones adjacent to narrow field margin habitats since it might be counterproductive to insist on the directive.

Data on the dimensions of watercourses and other aquatic habitats in Germany are available, theoretically allowing a Geographic Information System (GIS)-based application of plant protection products on arable land (Gutsche et al., 2004; Golla, personal communication). The position of the sprayer relative to a waterbody can be determined with the Global Positioning System (GPS). By the incorporation of the prescribed buffer zone width of the used product, data of the German spray drift model, and meteorological data (e.g. wind speed and direction) the nozzles can be automatically switched on or off – depending on the distance of the sprayer from surface water. This approach would ensure and facilitate the protection of aquatic habitats from pesticide drift (Golla et al., 2003, 2004; Gutsche et al., 2004). A prototype for the GPS-navigated application of plant protection products adjacent to waterbodies

might be developed by the German BBA after official authorisation (Golla, personal communication). Once more detailed data on terrestrial field margin habitats (e.g. width, quality) in Germany are available (based on digital data of the "Official Topographical-Cartographical Information System Germany" (ATKIS) or high-resolution aerial images (hr-images)), these might be used for an analogous GIS-based application of pesticides and incorporated into a local risk management scheme for terrestrial habitats (Kühne et al., 2000; Trapp et al., 2003). However, these detailed data are not available at present (Golla, personal communication).

Based on the significant effects of λ-cyhalothrin drift on *Coccinella septempunctata* L. larvae and coccinellid populations as well as the intermediate effects on adult *Aphidius colemani* Viereck found in the current study and the predictions made by Kühne et al. (2002) concerning possible risks for adult *C. septempunctata* and the predatory mite *Typhlodromus pyri* Scheuten it is suggested that spraying of λ-cyhalothrin close to any off-crop area that is likely to harbour populations of these beneficial arthropods should invariably be restricted. Although just few effects were observed, these should give cause for concern, since they may be indicative of the potential impact on non-target arthropods with equal levels of susceptibility towards λ-cyhalothrin. The ecotoxicological data of most beneficial arthropods and almost all "indifferent" species are not available so far (and possibly never will), but lack of information does not denote that they are not at risk.

6.2 Recovery of cereal aphid parasitoid populations through reimmigration

The release recovery experiment with *A. colemani* and the mark-release-recapture trials with protein-marked *Aphidius rhopalosiphi* DeStefani-Perez indicated that these species are able to disperse at least 16 m (*A. colemani*) and 48 m (*A. rhopalosiphi*) within one and two days, respectively. Although movement beyond these distances was not analysed, it is assumed that both parasitoid species are generally able to disperse much farther, as exemplified in sections 3.4.8 (page 107 et seqq.) and 5.4.6 (page 157 et seq.). Based on the current and previous (cf. 5.4.6) findings it is assumed that recovery of insecticide depleted parasitoid populations can take place via the process of immigration by specimens from surrounding habitats. However, it is important to recognise that the actual rates of immigration of aphid parasitoids into treated fields are supposed to be highly dependent on the availability of their aphid hosts (Smart et al., 1989; Holland et al., 2000). An aphid-free crop has a low

attractiveness to aphid parasitoids for two reasons. First, aphids are the prerequisite for reproduction, second, aphid honeydew is the essential food source for adult parasitoids. Both aphids and aphid honeydew can act as kairomones for aphid parasitoids and attract them to host habitats (Hågvar & Hofsvang, 1991). Aphid availability as prerequisite for reimmigration-mediated recovery of field populations of parasitoids has been indicated by Holland et al. (2000). Polyphagous predatory Carabidae reinvaded into dimethoate treated wheat fields, whereas the more specialised aphid parasitoids failed to recover to pre-treatment levels, as did their aphid hosts .

Furthermore, the mark-release-recapture trials with *A. rhopalosiphi* indicated that parasitoid dispersal is strongly influenced by climatic conditions. Wind and rain seemed to suppress the flight activity of released parasitoids. Previous studies have indicated similar results for other minute hymenopteran parasitoid species (cf. 5.4.4, page 152 et seqq.). Thus, if a pesticide treatment is followed by a rainy and windy (approximately > 2.5 m/s) period that reduces parasitoid dispersal activity, reduced or even no recovery of insecticide depleted field populations through immigration from surrounding habitats might occur.

However, the most important prerequisite for a reimmigration-mediated recovery of parasitoid populations is definitely the suitability of the surrounding habitats to act as source of parasitoids. Recent studies demonstrated that grassy field margin strips that provide alternative aphid hosts can serve as cereal aphid parasitoid reservoir (Langer & Hance, 2004; Levie et al., 2004). Similar results were found in the present study; due to the availability of cereal aphids in the field margins there were nearly no significant gradients in parasitoid densities from the margins into the crop areas.

Recovery of arthropod populations following insecticide treatments depends heavily on the persistence of the insecticidal activity. Results of the present work as well as previous studies suggest that the toxic effects of λ-cyhalothrin to *Aphidius* species are short-lived. Although this insecticide is inherently toxic to adult *A. rhopalosiphi* (Sterk et al., 1999), the toxic effects of λ-cyhalothrin to aphid parasitoids seem to be ephemeral, i.e. less than three days for *A. rhopalosiphi* (Jansen, 2001) and less than two days for *A. colemani* (Fiedler, unpublished). As a result, the rate of recovery through immigration is most likely not inhibited by persistent insecticidal toxicity. Furthermore, from laboratory studies it is known that the hatching rate of *A. uzbekistanicus* and *A. rhopalosiphi*, respectively, from λ-cyhalothrin treated mummies is not reduced (Krespi et al., 1991; Jansen, 1996). Thus, recovery of depleted field populations can be

accelerated by the emergence of parasitoids from remaining mummies some days subsequent to the application.

However, it cannot be excluded that the recovered parasitoid population might suffer from sublethal effects of λ-cyhalothrin, such as reductions in longevity and fertility, changes in sex ratio, sterility, changes in searching, feeding or oviposition behaviour (Krespi et al., 1991; Provost et al., 2003; Stark & Banks, 2003; Stark et al., 2004a,b). Krespi et al. (1991) analysed sublethal effects of λ-cyhalothrin on the cereal aphid parasitoid *Aphidius ervi* Haliday in the laboratory. If exposed for one hour to λ-cyhalothrin deposits, the longevity of both male and female parasitoids was significantly reduced. Furthermore, females produced a significantly lower percentage of female offspring.

6.3 Experimental design and arthropod monitoring methods

In field studies on the environmental effects of pesticides there is always the trade-off between plot size and replication (e.g. Sotherton et al., 1988; Smart et al., 1989; Perry, 1997). Sotherton et al. (1988) concluded that the plot size will influence the duration of effects since mobile groups might rapidly reimmigrate into treated plots, thereby masking treatment effects. This has been shown by Smart et al. (1989), who assessed effects of insecticides on arthropods using two different experimental designs, an unreplicated large-plot design (0.84 ha) and a replicated (three to five replications) small-plot design (0.02 to 0.13 ha). They concluded that the latter was useful to estimate effects on static organisms such as aphids, but not for the estimation of effects on more mobile groups (e.g. Carabidae or aphid parasitoids). The use of the large-plot design was recommended to analyse effects on mobile groups as well as on less abundant groups, based on the opinion that large plots allow more intensive sampling than small plots. Similar conclusions were drawn by Kennedy et al. (2001), who compared effects of insecticides on ground-dwelling predators in winter wheat using large open plots (0.89 ha) and small enclosed plots (0.01 ha). The number of individuals trapped per pitfall trap was higher in large plots than in small plots. Moreover, more species were recorded in large open plots compared with small enclosed plots. However, the differences in the capture efficacy of traps were not only related to the plot size but also to the enclosures. Arthropods were supposed to move along the barriers, possibly resulting in a low capture efficacy of traps positioned in the plot centres.

Although it is understood that the largest possible plot size should be used in field experiments, this should not be done at the expense of replications (Sotherton et al., 1988; Perry, 1997). In large-scale field studies on the environmental effects of pesticides land availability is almost always a limiting factor. However, while planning experiments, a compromise between statistical and ecological criteria has to be found that should lead to the most appropriate plot size (Sotherton et al., 1988). Prior to the start of the current study, two statisticians were consulted. Both strongly recommended to perform at least eight replicates to allow for reasonable statistical analysis (Bretz and Perry, respectively, personal communication). Due to the limited land available, the largest possible plot size was approximately 0.13 ha, i.e. less than suggested by Candolfi et al. (2000b), who recommended plot sizes of 1 ha but fewer replications (three to four). However, Candolfi et al. (2000b) as well as Kennedy et al. (2001) proposed large plots to avoid significant edge effects (i.e. through rapid recolonisation from surrounding habitats) when analysing side-effects of pesticides. But recovery through reimmigration from the field margin was on of the key questions of the current study. Reimmigration was measured on a relatively small scale, i.e. up to a distance of 25 m into the treated wheat, therefore the plot sizes were appropriate for this specific research question.

Perry (1997) pointed out that replicate plots should ideally be situated in one single field to keep between-plot heterogeneity as low as possible. However, in the present work it was impossible to meet this demand. Due to the limited land available, replicate plots had to be situated in three different fields. These fields had the same cropping history, as postulated by Candolfi et al. (2000b).

Every sampling method has its constraints; a certain method can be efficient for one arthropod group, whereas for another group it is not. The current work focused on insecticide effects on insects inhabiting the upper canopy strata, i.e. aphid parasitoids, plant dwelling predators (incl. non-predatory adult stages), and cereal aphids. Two separate sampling methods were used to estimate treatment effects on their population dynamics: visual counting and sweep netting. Both methods are relative methods of population measurement, i.e. they do not provide data on absolute population densities (Southwood & Henderson, 2000).

Visual counting of aphids and the different developmental stages of their natural enemies is a common methodology of estimating their population densities in wheat that has been used in countless earlier studies (e.g. Poehling, 1987; Longley et al., 1997a; Jansen, 2000; Freier et al. 2003, and many more). The advantage of counting is that it provides a large amount of data that is instantaneously available because no

time-consuming sample preparations and determinations in the laboratory are necessary. Furthermore, counting is relatively weather independent and does not require expensive equipment but just expertise in the identification of species. Counting is useful for estimating densities of non-mobile developmental stages (eggs and pupae) of insects that are not (or not efficiently) collected by other sampling methods such as sweep netting, suction sampling, or different kinds of traps (Sutherland, 1996). However, if natural enemy population densities are small, a large number of tillers have to be inspected to obtain a reasonable estimation of population densities (e.g. Freier et al., 2003). In that case, visual counting can be very time- and labour-intensive. In the current study 3,200 tillers were searched for insect stages on each monitoring date. Depending on the level of infestation it took three persons approximately eight hours to inspect the tillers. Another shortcoming of visual counting is that small predator stages such as first instar larvae might be overlooked. Furthermore, when disturbed, mobile insects like coccinellids or chrysopids might drop from the plant or, in the case of adults, fly off (Jansen, 2000). These limitations might lead to an underestimation of densities when counting is done carelessly. To overcome the drawbacks associated with visual counting, a second sampling method was performed, as proposed by Candolfi et al. (2000b).

An advantage of sweep netting is that leaf-dwelling insects from the upper canopy strata and flying insects that are entering/leaving the crop or flying closely above the crop (e.g. some hoverfly species in search for aphid colonies (Sutherland et al., 2001b)) can be sampled simultaneously. Moreover, sweep netting is carried out to collect less abundant groups, as it covers a relatively large area of the crop (Moreby et al., 2001). Further advantages of this sampling method are that it requires just little training, no specialised or expensive equipment, and that a large amount of data can easily be gathered by a single person. The drawback of sweep sampling is its dependence on weather conditions. Rain and/or wet foliage impede sweep netting, since caught insects may stick to the inside of the sweep net bag making it very difficult to remove them. Furthermore, it was experienced that sweep sampling cannot be properly performed at wind speeds of more than approximately 3 m/s. At these wind speeds the net is flapping and cannot be used properly. Sweep netting cannot be carried out in short vegetation (i.e. less than 15 cm high) or when the vegetation has been flattened by wind or rain (Sutherland, 1996). In addition, sweep netting does not work on thorny or very stiff vegetation, as the net might be damaged.

Suction sampling is another method that has been extensively used in the wheat agroecosystem to estimate population densities of both leaf dwelling predators and

flying insects such as aphid parasitoids (e.g. Longley et al., 1997a; Moreby et al., 2001). However, it was decided to perform sweep netting instead of suction sampling in the current work for several reasons. First, suction sampling only samples a small area, whereas sweep netting covers a wider area (see above). Second, by suction sampling dead organisms may also be collected (Moreby et al., 2001). Particularly following insecticide treatments the additional collection of dead insects can result in an underestimation of treatment effects. Third, suction sampling is most efficient in low vegetation (max. 15 cm, Sutherland, 1996), therefore in the later growth stages of the wheat (height of the wheat plants 80 cm) when samples were taken, this method may be less effective. Fourth, suction traps also collect soil and plant debris, which may result in the damage of small insects (Hagler et al., 2002a). Fifth, suction samplers can be heavy and the petrol tank has to be refilled at certain time intervals. Moreover, good flyers such as adult hoverflies are not efficiently captured by suction sampling, since they are able to evade the sampler (Sutherland, 1996). Like sweep netting, suction sampling can only be performed in dry vegetation. However, the advantage of suction sampling over sweep netting is that it also collects organisms that are dwelling in lower canopy strata or on the ground. Thus, this method can provide absolute population estimates by completely sampling an enclosed area. For example, Kühne et al. (2002) combined suction sampling with a covering method, i.e. they enclosed the vegetation with 1 x 1 m gauze cages ("biocoenometers"). Subsequent to suction sampling they entirely removed the vegetation inside the cages and checked plant material for remaining arthropods in the laboratory.

Numerous trapping methods are available that can be used for the capture of flying insects (for an overview refer to Mühlenberg, 1993; Sutherland, 1996 or Southwood & Henderson, 2001). Of these methods some are "active", i.e. organisms are attracted to the trap by colour, light, or bait, and some methods are "passive", i.e. organisms are captured more or less randomly without being attracted to the trap (Southwood & Henderson, 2000). Since it is known that various insect species are attracted to certain colours, this knowledge is not only used in biological plant protection (e.g. use of blue sticky traps for catching thrips and leafminers in greenhouses) but also to collect insects in field studies. Yellow or blue water pan traps or sticky traps have been widely used to catch flying insects such as adult coccinellids, hoverflies, aphid parasitoids or alate aphids (e.g. Southwood & Henderson, 2000; Stephens & Losey, 2004). However, due to their attractiveness coloured traps might catch more specimens (target and "non-target") than passive methods. Thereby they can provide data that are open to misinterpretation (Southwood & Henderson, 2000). For this reason, no coloured traps

were used in the current study. Prominent examples of passive methods for collecting flying insects are Malaise traps and flight interception traps such as window traps (Mühlenberg, 1993; Sutherland, 1996; Southwood & Henderson, 2000). Whereas Malaise traps are highly effective for various dipteran families and larger Hymenoptera, flight interception traps are particularly effective for collecting Coleoptera (Southwood & Henderson, 2000). However, their use in large field trials with a lot of sample positions is limited due to their expensiveness and difficulty of installation (Sutherland, 1996; Carrel, 2002). Moreover, in the current study the possibility to install relatively tall and complex traps was limited since they might have interfered with the farmer's work.

If sampling is restricted to relatively large insects, such as coccinellids or hoverflies, densities can also be estimated by timed counts while walking at a constant velocity through a defined part of the field (e.g. Michels et al., 1997). However, this procedure was inadequate for use in the present study because hymenopteran aphid parasitoids or early instars of leaf-dwelling predators are too small to be recognised while walking through the plots. Moreover, this method does not provide samples of specimens, which is often essential for proper species identification.

A commonly used method for the collection of leaf dwelling insects is the beating method, i.e. the plants are hit with a stick so that the arthropods on the plant are dislodged and drop into a container that is placed beneath the plant (e.g. Sutherland, 1996; Southwood & Henderson, 2000). The advantage of this method over sweep netting is that it also collects insects that dwell in the lower crop strata. Jansen (2000) used this method successfully to estimate densities of chrysopid, coccinellid and syrphid larvae, and adult coccinellids in wheat. Moreover, this method can be used to estimate numbers of insects that are killed by an insecticide treatment, by collecting dead insects right after the spray (Jansen, 2000). However, this method is not suitable for the collection of flying insects, as they might escape (Sutherland, 1996).

The drawback of sweep netting and the other trapping methods mentioned above is that a large amount of additional catches of "indifferent" organisms are made. These additional catches can be reduced in future studies by using more selective methods. For the capture of small hymenopteran parasitoids, Hagler et al. (2002a) recently proposed the usage of small stationary battery-operated suction traps. These traps were used in mark-release-recapture studies, where they efficiently captured the minute target insects but were not powerful enough to capture large "non-target" insects. The usage of such relative selective traps does not only save the lives of many insects, but, due to a decrease in additional catches, it can also reduce the time that the researcher has to spent to sort samples in the lab. Furthermore, traps can be used

to sample parasitoids at different heights within the canopy. However, the use of these suction traps in large-scale field studies that require a lot of sample positions might be limited; both the production of the traps and the frequent need to replace batteries is time- and cost-intensive (Hagler et al., 2002a). However, no selective and passive traps for the other groups that were investigated in the current study (adult and larval chrysopids, coccinellids, and syrphids) are available so far.

In the release-recapture trial using *A. colemani*, aphid infested trap plants were used to estimate the initial dispersal of released parasitoids. Aphid infested trap plants have been used in previous studies on the dispersal of aphid parasitoids (Fernandes et al., 1997; Muratori et al., 2000). Furthermore, trap plants have been utilised to estimate activity of naturally occurring parasitoids in arable fields (Milne, 1995). For (mark-) release-recapture studies the use of trap plants is advantageous because this method does not reduce the number of released parasitoids by catching or trapping, thereby providing information on the persistence of released organisms at the release site. Furthermore, it gives information of both dispersal and parasitism. However, a disadvantage of using aphid infested trap plants in dispersal studies with aphid parasitoids is that the movement of females but not of males can be determined. Moreover, it is not possible to relate parasitism events to the number of specimens that actually were engaged in dispersal. In the current study, for instance, released female *A. colemani* could have parasitised aphids on a local scale (e.g. on a single plant) but they also could have distributed their eggs on a larger scale (e.g. on several plants). Therefore, mummies found on single trap plants could originate from a single female or several females. However, in future studies this problem might possibly be solved by the use of molecular DNA markers (e.g. MacDonald & Loxdale, 2004). Another limiting factor is that the use of aphid infested trap plants is very time- and labour-intensive. It requires extensive preparatory work to rear plants and aphids, and to infest a large number of trap plants with aphids. Moreover, under the current experimental conditions (stubble fields), trap plants were very susceptible to be damaged by mammalian herbivores. Therefore, the experimental set-ups had to be fenced in, which was not only labour- but also money-intensive. Furthermore, if trap plants are planted in pots it might be necessary to water them at frequent intervals (Milne, 1995). This can be a great problem at remote experimental sites.

In the dispersal studies conducted in 2002 to 2004 immunomarked parasitoids were released; this approach required a recapture method that provided individual specimens for the detection of the immunomarker. Thus, sweep netting and sticky

traps were used to recapture IgG-marked *A. rhopalosiphi*. Both methods are the most commonly used techniques to recapture hymenopteran parasitoids in mark-release-recapture studies (Hagler et al., 2002a). Reasons for the use of the sweep net are given above. The initial dispersal of parasitoids right after their release was estimated by means of sticky traps, which easily permitted sampling from different canopy positions. In 2004, only sticky traps were used for the recapture of IgG-marked parasitoids since it was thought to increase the amount of recapture by the use of a sampling method that is relatively unsusceptible to adverse weather conditions. In preliminary experiments sticky traps had been used successfully to capture aphid parasitoids in spite of wind and rain; it had been shown that aphid parasitoids stick on wet insect glue. Furthermore, sticky traps capture specimens continuously (e.g. for 24 hours), whereas sweep netting represents a moment in time. Therefore, the former method might provide more stable data. Stephens and Losey (2004) compared the effectiveness of yellow sticky traps, sweep netting and visual searching for coccinellid sampling. Sticky cards were most efficient, which was explained by their long exposure period. However, the attractiveness of yellow cards to coccinellids additionally increased the efficiency of this sampling method compared to the passive methods. Aphid parasitoids are also attracted to yellow (Hågvar & Hofsvang, 1991). However, the use of yellow sticky traps to attract *A. rhopalosiphi* and thereby enhance the amount of recaptured specimens was no option for the current study, because the aim was not to attract released parasitoids to certain sites but to estimate their dispersal without manipulation.

For future mark-release-recapture studies the use of sticky traps may be preferred over sweep netting for the above mentioned reasons. In order to increase the amount of recapture the set up of more traps, both in horizontal direction within the canopy and in vertical direction within the crop, is urgently necessary. However, since sticky traps do not capture selectively, the use of the suction traps described by Hagler et al. (2002a) (see above) can be an alternative recapture method to increase recapture of released wasps and simultaneously avoid the collection of additional specimens.

7. SUMMARY

Pesticide spray drift is one of the most relevant routes of contamination of field margin habitats. In intensively managed agricultural landscapes these (semi-) natural habitat types enjoy important environmental and conservation functions. They can be permanent or temporary habitats for important natural enemies of insect pests; since natural enemies are thought to disperse from field margins into the adjoining crops, they may contribute to the reduction of pest outbreaks or to repopulation of insecticide depleted populations in adjacent arable field crops. So far, only limited data on the effects of insecticide drift on terrestrial non-target arthropods within field margin habitats and the recovery of field populations through reimmigration of specimens from field margins are available. Therefore, the main objectives of the current work were (1) to quantify insecticide drift deposition on off-crop plant surfaces and to analyse the effect of drift deposits on non-target arthropods, (2) to estimate the effects of drift on population dynamics of insects within field margins as well as to investigate the post-treatment recovery of insect populations in adjacent wheat fields, and (3) to estimate the reimmigration ability of aphid parasitoids by conducting dispersal studies under field conditions.

Drift of the pyrethroid Trafo® (λ-cyhalothrin) into 3 m wide field margins bordering conventionally farmed winter wheat fields in Lower Saxony, Germany, was investigated. Field margin strips were divided into 16 plots of equal size (approximately 54 m). A control and a drift-treatment were performed; these were randomly distributed among the field margin plots. Each treatment was replicated eight times. During insecticide application control plots were covered with polythene sheets to prevent contamination due to insecticide drift, whereas drift plots were left uncovered. Insecticide (drift) deposition on leaf surfaces of broad beans, *Vicia faba* L., exposed within field margins at 1, 2, and 3 m distance from the field edge and directly within the crop was quantified using the fluorescent tracer sodium fluorescein. The toxicity of off-crop and within-crop deposits to aphid parasitoids, *Aphidius colemani* Viereck (Hymenoptera: Braconiade), and ladybeetle larvae, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), was estimated. Drift deposits on leaf surfaces were detected up to 3 m from the field edge. Deposits were highly variable, but tendentiously decreased with increasing distance from the field edge. Mean corrected mortalities of *A. colemani* were < 50 % (1 m) and < 30 % (2 and 3 m) 12 and 24 hours post-exposure to drift deposits. *C. septempunctata*-larvae were more susceptible to drift deposits of λ-cyhalothrin, showing mortality < 80 % (1 m), ≤ 67 % (2 m), and ≤ 52 % (3 m) 12 and 24 hours after exposure. High positive correlation coefficients proved the relationship

between deposits of λ-cyhalothrin on leaf surfaces and mortalities of test organisms. Results indicate that individual specimens of *C. septempunctata* and *A. colemani* may be endangered by drift of λ-cyhalothrin at least up to a distance of 3 m from the sprayed crop. Due to their higher susceptibility and their faster reaction to λ-cyhalothrin, mortality risks for *C. septempunctata*-larvae might be higher compared to adult *A. colemani*.

Possible effects on populations of aphid parasitoids and coccinellids cannot be elaborated from mortality tests alone but require verification through field-based studies. Therefore, further investigations were carried out to estimate the effects of λ-cyhalothrin drift on the population dynamics of aphids and selected groups of their natural enemies, i.e. plant dwelling predators of the families Coccinellidae, Chrysopidae, and Syrphidae, and cereal aphid parasitoids of the family Braconidae, in the field margins. The field-based surveys detected a negative impact of λ-cyhalothrin drift into the margins on the population dynamics of arthropods with high susceptibility to this insecticide, i.e. coccinellids and the target pest (cereal aphids). Whereas aphid populations showed a rapid (within ten days) recovery from drift effects, recovery of coccinellid populations was slower (approximately four weeks). No significant drift effects on chrysopids, syrphids, and aphid parasitoids were noticed. This was explained by low or intermediate susceptibility of these organisms to λ-cyhalothrin (e.g. chrysopids) as well as by rapid population recovery through immigration of highly mobile stages from surrounding habitats (e.g. syrphid flies).

However, drift effects on the sensitive indicator organisms (i.e. coccinellids and aphids) indicate that non-target arthropods with comparable levels of susceptibility towards λ-cyhalothrin (e.g. linyphiid and lycosid spiders, mites) might be negatively affected by drift of this insecticide.

In addition to drift effects on populations within field margins, within-field reimmigration/recovery trends in insect populations (aphids and developmental stages of chrysopids, coccinellids, syrphids, and aphid parasitoids) in wheat areas adjacent to drift-contaminated and drift-protected field margins were analysed. Population densities were estimated weekly at 4 and 24 m into the wheat by standardised sweep net samples as well as at 5 and 25 m into the wheat by visual counts of arthropods on wheat tillers. The analysis of population recovery revealed significantly higher cereal aphid population densities in wheat areas at close distance from uncontaminated control field margin strips than at farther distance into the wheat, indicating that control field margins possibly acted as a source of “aphid colonists” that immigrated into the adjacent crop. This tendency was just observed at functional group level but not at the

species level. Drift-contaminated field margin strips did not significantly influence cereal aphid densities in adjacent wheat areas. Densities of aphidophagous syrphid flies were significantly higher in field margins than in adjacent wheat areas in both control and drift field plots. Significantly higher densities of hoverflies in wheat areas at 4 than at 24 m from the field edge indicated a temporary migration of syrphids between field margins and the adjacent crop. Control and drift-contaminated field margin strips did not differently influence syrphid densities in wheat. In contrast to numbers of adult hoverflies, syrphid eggs were evenly distributed across field margins and adjacent wheat areas in both control and drift treatment. Initially following the insecticide treatment, syrphid egg densities were significantly influenced by aphid densities but not by the distance from the field edge demonstrating the importance of host availability for the (re)invasion of syrphids into fields following an insecticide application. Overall, no spatial trend in cereal aphid parasitoid recovery in wheat fields following the insecticide application was detected in both control and drift plots. Parasitoids were equally distributed amongst field margins and adjacent wheat areas, as were mummified aphids on most monitoring dates. Although λ-cyhalothrin is classified as harmless to populations of *C. carnea* (Stephens), initially reduced densities of adult *C. carnea* in wheat areas adjacent to both drift-contaminated and control field margins following the treatment indicated an effect of the insecticide. This effect was ephemeral and followed by a large increase in densities within field margins and wheat areas of control and drift treatment, respectively. Overall, field margins had no significant effect on the within-field densities of adult *C. carnea*; the same applied to chrysopid egg and larval densities. The application of λ-cyhalothrin almost totally reduced within-field densities of aphidophagous coccinellids for a period of approximately three weeks. During this time, coccinellid stages were just (with one exception) collected within field margins, demonstrating the shelter function of field margins for ladybeetles. One month subsequent to the application of λ-cyhalothrin to wheat fields, coccinellid populations in both control and drift plots numerically recovered to pre-treatment densities. Higher, although insignificantly, densities of Coccinellidae at 4 m than at 24 m indicated a possible immigration of coccinellids from the field margin into the wheat.

As a result, the current work showed the need to minimise potential risks arising from insecticide spray drift into terrestrial off-crop habitats, e.g. through appropriate drift mitigation strategies (i.e. use of low-drift nozzles, incorporation of buffer zones, and spraying at acceptable weather conditions).

Reinvasion processes into field crops following insecticide applications are inextricably linked with species dispersal capacity. The reimmigration potential of natural enemies

was investigated in detail using aphid parasitoids as model organisms. Parasitoid dispersal ability was estimated by dispersal studies conducted under field conditions. The first study assessed the dispersal of female *A. colemani* after point release on the basis of mummified aphids on trap plants deployed equidistantly on circles at distances of 1, 2, 4, 8, and 16 m from a central release point. Plants were replaced on days 1 and 3 after the release of *A. colemani*. Since this species does not naturally occur in the experimental area, all *A. colemani* mummies that were collected from trap plants were assigned to released parasitoids. The pattern of mummified aphids showed that parasitoids moved at least 16 m within 24 hours after release. Mean numbers of mummies per trap plant were low (3.0, 1.8, and 1.1 on days 1, 3, and 5 after release). In most cases dispersal was random with regard to the compass direction. Prevailing light to moderate wind speeds did not influence dispersal of parasitoids. Released *A. colemani* were persistent at the experimental site for at least three days. Results suggest that mated and experienced *A. colemani* generally tend to disperse immediately after release, as they evenly dispersed on a circular area with 16 m radius within one day. Mummy densities indicated that a relatively low number of released *A. colemani* remained at the release site and that the majority of released parasitoids dispersed much farther than 16 m.

Whereas the dispersal study with *A. colemani* was conducted under “artificial” conditions on freshly harvested fields to exclude conspecifics, hyperparasitoids, or predators, a second dispersal study was carried out under “realistic” field conditions in a typical agricultural landscape. In this study, the use of a mark-release-recapture technique allowed the estimation of the dispersal of both female and male aphid parasitoids. The species *Aphidius rhopalosiphi* DeStefani-Perez, an important natural enemy of cereal aphids in the German wheat agroecosystem, was used as a model organism. Parasitoids were marked with a mammalian protein, rabbit immunoglobulin G (IgG), by feeding them an IgG-enriched honey solution. The present study showed that adult aphid parasitoids can be reliably marked with IgG. Parasitoids retained detectable amounts of the IgG over their whole lifespan (i.e. eight days) and seemed not to be negatively affected by the marker. For dispersal studies several thousand IgG-marked *A. rhopalosiphi* were released at the field edge of a winter wheat field; the temporal and spatial dispersal patterns of parasitoids were estimated by recaptures with a sweep net (2002), a combination of sweep net and sticky traps (2003) and only sticky traps (2004) at different distances (2 to 48 m) into the wheat one to five days following the release. Total recaptures of released *A. rhopalosiphi* amounted to 0.28 % (2002), 1.12 % (2003), and 1.22 % (2004). Results demonstrated that *A. rhopalosiphi* moved from the field margin into the wheat. Individual specimens were able to disperse

over a distance of at least 24 m within one day and 48 m within two days, respectively. The persistence of released *A. rhopalosiphi* at the release site seemed to be relatively low. More than 94 % of recaptures were made within the first 48 hours after release. Furthermore, the mark-release-recapture trials showed that the movement of aphid parasitoids greatly depends on weather conditions. Wind and rain seemed to suppress the flight activity of released specimens, resulting in low numbers of recaptured wasps. In 2003 and 2004 sticky traps were placed at 2 m from the central release point at three different heights (ground-level, ear-level, 3 m) in order to investigate the initial dispersal of immunomarked *A. rhopalosiphi*. Virtually all recaptured parasitoids were caught by traps placed at ground-level, which was explained by the adverse weather conditions (wind, rain, and cloudiness) during the course of the 2003 and 2004 mark-release-recapture trails. Overall, recapture patterns of released *A. rhopalosiphi* did not indicate differences in the dispersal behaviour of males and females.

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9. APPENDIX

9.1 Results of statistical tests

Tab. A1. Results ATS. Test for differences in spray and spray drift deposits on leaves at different distances from the sprayed crop. Differences are significant at an adjusted p-value of 0.0083 (bold type).

		top-leaves			bottom-leaves	
field 1&2 2002	df	F	p	df	F	p
test of distance effect	48	79.40	**< 0.0001**	48	47.23	**< 0.0001**
contrasts:						
field vs. 1 m	48	43.35	**< 0.0001**	48	4.92	0.0312
field vs. 2 m	48	140.89	**< 0.0001**	48	71.06	**< 0.0001**
field vs. 3 m	48	220.80	**< 0.0001**	48	113.24	**< 0.0001**
1 m vs. 2 m	48	24.44	**< 0.0001**	48	33.75	**< 0.0001**
1 m vs. 3 m	48	59.92	**< 0.0001**	48	62.07	**< 0.0001**
2 m vs. 3 m	48	7.82	**0.0074**	48	4.28	0.0439
field 3 2002	df	F	p	df	F	p
test of distance effect	48	42.77	**< 0.0001**	48	31.46	**< 0.0001**
contrasts:						
field vs. 1 m	48	34.66	**< 0.0001**	48	1.29	0.2614
field vs. 2 m	48	88.33	**< 0.0001**	48	44.62	**< 0.0001**
field vs. 3 m	48	114.67	**< 0.0001**	48	70.25	**< 0.0001**
1 m vs. 2 m	48	10.79	**0.0019**	48	26.88	**< 0.0001**
1 m vs. 3 m	48	20.34	**< 0.0001**	48	45.93	**< 0.0001**
2 m vs. 3 m	48	1.50	0.2265	48	2.53	0.118
field 1&2 2003	df	F	p	df	F	p
test of distance effect	48	28.06	**< 0.0001**	48	19.70	**< 0.0001**
contrasts:						
field vs. 1 m	48	29.80	**< 0.0001**	48	1.25	0.2696
field vs. 2 m	48	57.09	**< 0.0001**	48	27.31	**< 0.0001**
field vs. 3 m	48	76.75	**< 0.0001**	48	46.33	**< 0.0001**
1 m vs. 2 m	48	3.85	0.0556	48	14.77	**0.0004**
1 m vs. 3 m	48	9.54	**0.0033**	48	28.32	**< 0.0001**
2 m vs. 3 m	48	1.27	0.2652	48	2.19	0.1458
field 3 2003	df	F	p	df	F	p
test of distance effect	48	37.16	**< 0.0001**	48	25.93	**< 0.0001**
contrasts:						
field vs. 1 m	48	41.46	**< 0.0001**	48	23.09	**< 0.0001**
field vs. 2 m	48	71.07	**< 0.0001**	48	47.14	**< 0.0001**
field vs. 3 m	48	104.72	**< 0.0001**	48	72.98	**< 0.0001**
1 m vs. 2 m	48	3.47	0.0686	48	3.82	0.0566
1 m vs. 3 m	48	12.60	**0.0009**	48	12.57	**0.0009**
2 m vs. 3 m	48	2.84	0.0982	48	2.53	0.1182

Tab. A1 (continued).

		top-leaves			bottom-leaves	
field 1&2 2002	df	F	p	df	F	p
test of distance effect	48	79.40	**< 0.0001**	48	47.23	**< 0.0001**
contrasts:						
field vs. 1 m	48	43.35	**< 0.0001**	48	4.92	0.0312
field vs. 2 m	48	140.89	**< 0.0001**	48	71.06	**< 0.0001**
field vs. 3 m	48	220.80	**< 0.0001**	48	113.24	**< 0.0001**
1 m vs. 2 m	48	24.44	**< 0.0001**	48	33.75	**< 0.0001**
1 m vs. 3 m	48	59.92	**< 0.0001**	48	62.07	**< 0.0001**
2 m vs. 3 m	48	7.82	**0.0074**	48	4.28	0.0439
field 3 2002	df	F	p	df	F	p
test of distance effect	48	42.77	**< 0.0001**	48	31.46	**< 0.0001**
contrasts:						
field vs. 1 m	48	34.66	**< 0.0001**	48	1.29	0.2614
field vs. 2 m	48	88.33	**< 0.0001**	48	44.62	**< 0.0001**
field vs. 3 m	48	114.67	**< 0.0001**	48	70.25	**< 0.0001**
1 m vs. 2 m	48	10.79	**0.0019**	48	26.88	**< 0.0001**
1 m vs. 3 m	48	20.34	**< 0.0001**	48	45.93	**< 0.0001**
2 m vs. 3 m	48	1.50	0.2265	48	2.53	0.118
field 1&2 2003	df	F	p	df	F	p
test of distance effect	48	28.06	**< 0.0001**	48	19.70	**< 0.0001**
contrasts:						
field vs. 1 m	48	29.80	**< 0.0001**	48	1.25	0.2696
field vs. 2 m	48	57.09	**< 0.0001**	48	27.31	**< 0.0001**
field vs. 3 m	48	76.75	**< 0.0001**	48	46.33	**< 0.0001**
1 m vs. 2 m	48	3.85	0.0556	48	14.77	**0.0004**
1 m vs. 3 m	48	9.54	**0.0033**	48	28.32	**< 0.0001**
2 m vs. 3 m	48	1.27	0.2652	48	2.19	0.1458
field 3 2003	df	F	p	df	F	p
test of distance effect	48	37.16	**< 0.0001**	48	25.93	**< 0.0001**
contrasts:						
field vs. 1 m	48	41.46	**< 0.0001**	48	23.09	**< 0.0001**
field vs. 2 m	48	71.07	**< 0.0001**	48	47.14	**< 0.0001**
field vs. 3 m	48	104.72	**< 0.0001**	48	72.98	**< 0.0001**
1 m vs. 2 m	48	3.47	0.0686	48	3.82	0.0566
1 m vs. 3 m	48	12.60	**0.0009**	48	12.57	**0.0009**
2 m vs. 3 m	48	2.84	0.0982	48	2.53	0.1182

Tab. A2. Results ATS. Test for differences in control-corrected mortalities (Schneider-Orelli) of *A. colemani* 12 and 24 hours, respectively, after exposure to λ-cyhalothrin deposits at different distances from the field edge. Differences are significant at an adjusted p-value of 0.0083 (bold type).

		12h post-exposure				
		top-leaves			bottom-leaves	
field 1&2 2002	df	F	p	df	F	p
test of distance effect	16	1.00	0.416	16	0.48	0.6946
contrasts:						
field vs. 1 m	16	1.14	0.3009	16	0.76	0.3950
field vs. 2 m	16	0.67	0.4245	16	0.11	0.7411
field vs. 3 m	16	3.43	0.0824	16	0.14	0.7164
1 m vs. 2 m	16	0.05	0.8317	16	0.22	0.6476
1 m vs. 3 m	16	0.46	0.5069	16	1.16	0.2973
2 m vs. 3 m	16	0.80	0.3841	16	0.37	0.5495

		24h post-exposure				
		top-leaves			bottom-leaves	
field 1&2 2002	df	F	p	df	F	p
test of distance effect	16	0.68	0.5692	16	0.20	0.8896
contrasts:						
field vs. 1 m	16	0.21	0.6505	16	0.04	0.8446
field vs. 2 m	16	0.76	0.3960	16	0.58	0.4561
field vs. 3 m	16	2.21	0.1562	16	0.28	0.6025
1 m vs. 2 m	16	0.13	0.7269	16	0.24	0.6315
1 m vs. 3 m	16	0.79	0.3873	16	0.08	0.7773
2 m vs. 3 m	16	0.28	0.6012	16	0.04	0.8430

		12h post-exposure				
		top-leaves			bottom-leaves	
field 1&2 2003	df	F	p	df	F	p
test of distance effect	16	0.81	0.5029	16	0.93	0.4464
contrasts:						
field vs. 1 m	16	0.28	0.6012	16	0.13	0.7227
field vs. 2 m	16	0.83	0.3754	16	0.71	0.4119
field vs. 3 m	16	0.45	0.5118	16	0.83	0.3756
1 m vs. 2 m	16	0.11	0.7473	16	1.09	0.3127
1 m vs. 3 m	16	1.09	0.3125	16	0.23	0.6401
2 m vs. 3 m	16	1.88	0.1894	16	2.31	0.1483

		24h post-exposure				
		top-leaves			bottom-leaves	
field 1&2 2003	df	F	p	df	F	p
test of distance effect	16	0.68	0.5692	16	0.20	0.8896
contrasts:						
field vs. 1 m	16	0.21	0.6505	16	0.04	0.8446
field vs. 2 m	16	0.76	0.3960	16	0.58	0.4561
field vs. 3 m	16	2.21	0.1562	16	0.28	0.6025
1 m vs. 2 m	16	0.13	0.7269	16	0.24	0.6315
1 m vs. 3 m	16	0.79	0.3873	16	0.08	0.7773
2 m vs. 3 m	16	0.28	0.6012	16	0.04	0.8430

Tab. A2 (continued).

	12h post-exposure					
	top-leaves			bottom-leaves		
field 3 2003	df	F	p	df	F	p
test of distance effect	16	1.94	0.1642	16	2.89	0.0693
contrasts:						
field vs. 1 m	16	3.42	0.0828	16	6.78	0.0192
field vs. 2 m	16	5.21	0.0364	16	0.08	0.7828
field vs. 3 m	16	4.69	0.0458	16	0.46	0.5057
1 m vs. 2 m	16	0.14	0.7126	16	6.24	0.0238
1 m vs. 3 m	16	0.07	0.7885	16	2.77	0.1154
2 m vs. 3 m	16	0.01	0.9198	16	0.69	0.4174

	24 h post-exposure					
	top-leaves			bottom-leaves		
field 3 2003	df	F	p	df	F	p
test of distance effect	16	3.33	**0.0434**	16	5.14	**0.0118**
contrasts:						
field vs. 1 m	16	1.68	0.2135	16	0.03	0.8583
field vs. 2 m	16	9.40	**0.0074**	16	8.96	0.0086
field vs. 3 m	16	7.64	0.0138	16	10.08	**0.0059**
1 m vs. 2 m	16	2.35	0.1447	16	5.93	0.0269
1 m vs. 3 m	16	1.62	0.2217	16	6.72	0.0196
2 m vs. 3 m	16	0.07	0.7968	16	0.02	0.8771

Tab. A3. Results ATS. Test for differences in control-corrected mortalities (Schneider-Orelli) of *C. septempunctata* 3, 12, and 24 hours after exposure to λ-cyhalothrin deposits at different distances from the field edge. Differences are significant at an adjusted p-value of 0.0083 (bold type).

	3 h post-exposure			12 h post-exposure			24 h post-exposure		
field 1&2 2003	df	F	p	df	F	p	df	F	p
test of distance effect:	16	9.91	**0.0007**	16	1.34	0.2956	16	3.33	0.0477
contrasts:									
field vs. 1 m	16	3.89	0.0660	16	1.21	0.2870	16	2.14	0.1632
field vs. 2 m	16	13.61	**0.0020**	16	1.30	0.2718	16	3.26	0.0898
field vs. 3 m	16	31.74	**< 0.0001**	16	4.69	0.0458	16	11.53	**0.0037**
1 m vs. 2 m	16	2.21	0.1567	16	0.00	0.9750	16	0.09	0.7697
1 m vs. 3 m	16	10.05	**0.0059**	16	0.85	0.3702	16	2.81	0.1133
2 m vs. 3 m	16	2.84	0.1116	16	0.79	0.3865	16	1.90	0.1873
field 3 2003	df	F	p	df	F	p	df	F	p
test of distance effect:	16	11.56	**0.0003**	16	24.98	**< 0.0001**	16	32.82	**< 0.0001**
contrasts:									
field vs. 1 m	16	0.14	0.7123	16	5.76	0.0289	16	8.88	0.0089
field vs. 2 m	16	18.51	**0.0005**	16	48.26	**< 0.0001**	16	53.72	**< 0.0001**
field vs. 3 m	16	18.51	**0.0005**	16	66.02	**< 0.0001**	16	95.82	**< 0.0001**
1 m vs. 2 m	16	16.41	**0.0009**	16	15.51	**0.0012**	16	14.20	**0.0017**
1 m vs. 3 m	16	16.41	**0.0009**	16	24.59	**0.0001**	16	34.78	**< 0.0001**
2 m vs. 3 m	16	0.00	1.0000	16	1.04	0.3225	16	4.54	0.0491

Tab. A4. Results ATS. Test for differences in arthropod densities within the field margin strip (0 m) and at 5 and 25 m (count data) and 4 and 24 m (sweep net data), respectively, into the wheat in the drift and control treatment subsequent to the application of λ-cyhalothrin to wheat fields. Differences are significant at an adjusted p-value of 0.0167.

Count data 2002

Cereal aphids

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	10.97	<.0001
pre-treatment dens.	20	0.01	0.9224
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	13.58	0.0002
0 vs. 25	20	13.74	0.0002
5 vs. 25	20	0.00	0.9885

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	13.01	<.0001
pre-treatment dens.	20	1.44	0.2305
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	6.48	0.0109
0 vs. 25	20	21.12	<.0001
5 vs. 25	20	8.88	0.0029

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.36	0.0422
pre-treatment dens.	20	0.04	0.8340
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.86	0.0494
0 vs. 25	20	4.48	0.0344
5 vs. 25	20	0.04	0.8368

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.50	0.0885
pre-treatment dens.	20	0.05	0.8254
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.10	0.0430
0 vs. 25	20	2.21	0.1374
5 vs. 25	20	0.36	0.5499

R. padi

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.78	0.0360
pre-treatment dens.	20	1.05	0.3044
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.72	0.0538
0 vs. 25	20	4.87	0.0273
5 vs. 25	20	0.26	0.6084

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.89	0.0310
pre-treatment dens.	20	1.37	0.2419
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.19	0.0739
0 vs. 25	20	5.59	0.0181
5 vs. 25	20	0.98	0.3232

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	12.99	<.0001
pre-treatment dens.	20	0.03	0.8647
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	13.95	0.0002
0 vs. 25	20	15.79	<.0001
5 vs. 25	20	0.19	0.6609

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	11.85	<.0001
pre-treatment dens.	20	0.45	0.5036
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	17.22	<.0001
0 vs. 25	20	9.39	0.0022
5 vs. 25	20	3.41	0.0650

Tab. A4 (continued).

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.35	0.1036
pre-treatment dens.	20	0.09	0.7589
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.71	0.3979
0 vs. 25	20	3.89	0.0486
5 vs. 25	20	2.58	0.1085

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	7.60	0.0019
pre-treatment dens.	20	0.13	0.7159
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.18	0.1395
0 vs. 25	20	11.56	0.0007
5 vs. 25	20	12.53	0.0004

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.01	0.9781
pre-treatment dens.	20	0.10	0.7475
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.03	0.8705
0 vs. 25	20	0.01	0.9432
5 vs. 25	20	0.01	0.9089

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.96	0.0664
pre-treatment dens.	20	0.15	0.7019
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.47	0.0626
0 vs. 25	20	3.46	0.0628
5 vs. 25	20	0.00	0.9992

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.27	0.2767
pre-treatment dens.	20	2.59	0.1073
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.69	0.1939
0 vs. 25	20	1.48	0.2242
5 vs. 25	20	0.02	0.9002

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.64	0.2008
pre-treatment dens.	20	3.00	0.0831
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.56	0.2123
0 vs. 25	20	2.15	0.1423
5 vs. 25	20	0.16	0.6856

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.59	0.0326
pre-treatment dens.	20	3.82	0.0505
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	5.58	0.0181
0 vs. 25	20	3.58	0.0585
5 vs. 25	20	0.23	0.6294

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.71	0.0811
pre-treatment dens.	20	2.60	0.1069
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.37	0.1236
0 vs. 25	20	3.82	0.0508
5 vs. 25	20	0.50	0.4780

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	4.35	0.0176
pre-treatment dens.	20	1.47	0.2253
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.99	0.0458
0 vs. 25	20	6.53	0.0106
5 vs. 25	20	0.62	0.4309

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	5.92	0.0069
pre-treatment dens.	20	3.17	0.0750
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	6.14	0.0132
0 vs. 25	20	7.40	0.0065
5 vs. 25	20	0.20	0.6547

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.02	0.1386
pre-treatment dens.	20	2.51	0.1132
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.22	0.1361
0 vs. 25	20	2.84	0.0921
5 vs. 25	20	0.13	0.7135

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.72	0.4527
pre-treatment dens.	20	0.74	0.3894
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.67	0.4141
0 vs. 25	20	0.98	0.3220
5 vs. 25	20	0.09	0.7654

Tab. A4 (continued).

S. avenae

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.20	0.0408
pre-treatment dens.	20	1.89	0.1695
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.88	0.1701
0 vs. 25	20	6.39	0.0115
5 vs. 25	20	1.36	0.2443

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.93	0.1454
pre-treatment dens.	20	0.06	0.8134
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.58	0.0585
0 vs. 25	20	1.71	0.1906
5 vs. 25	20	0.41	0.5199

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	18.35	<.0001
pre-treatment dens.	20	3.04	0.0810
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	27.87	<.0001
0 vs. 25	20	28.47	<.0001
5 vs. 25	20	0.04	0.8511

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	10.71	<.0001
pre-treatment dens.	20	0.09	0.7592
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	19.59	<.0001
0 vs. 25	20	10.25	0.0014
5 vs. 25	20	1.87	0.1711

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.18	0.3071
pre-treatment dens.	20	5.38	0.0204
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.00	0.9784
0 vs. 25	20	1.80	0.1795
5 vs. 25	20	1.66	0.1981

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.88	0.4144
pre-treatment dens.	20	0.15	0.6941
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.51	0.4751
0 vs. 25	20	1.82	0.1777
5 vs. 25	20	0.36	0.5495

M. dirhodum

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.24	0.7849
pre-treatment dens.	20	0.17	0.6776
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.46	0.4959
0 vs. 25	20	0.20	0.6531
5 vs. 25	20	0.06	0.8124

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.73	0.1769
pre-treatment dens.	20	3.88	0.0490
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9146
0 vs. 25	20	2.49	0.1149
5 vs. 25	20	2.84	0.0918

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.20	0.8161
pre-treatment dens.	20	0.88	0.3472
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.30	0.5830
0 vs. 25	20	0.31	0.5805
5 vs. 25	20	0.00	0.9996

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.94	0.3903
pre-treatment dens.	20	8.06	0.0045
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.79	0.1815
0 vs. 25	20	0.47	0.4932
5 vs. 25	20	0.50	0.4810

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.38	0.6866
pre-treatment dens.	20	0.31	0.5754
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.27	0.6024
0 vs. 25	20	0.11	0.7364
5 vs. 25	20	0.75	0.3875

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.26	0.7737
pre-treatment dens.	20	1.50	0.2208
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.36	0.5512
0 vs. 25	20	0.40	0.5248
5 vs. 25	20	0.00	0.9874

Tab. A4 (continued).

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.55	0.5745
pre-treatment dens.	20	6.21	0.0127
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.09	0.2974
0 vs. 25	20	0.07	0.7856
5 vs. 25	20	0.53	0.4673

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.12	0.3277
pre-treatment dens.	20	0.00	0.9458
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.20	0.6559
0 vs. 25	20	2.13	0.1442
5 vs. 25	20	1.03	0.3103

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.43	0.6476
pre-treatment dens.	20	0.00	0.9850
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.80	0.3701
0 vs. 25	20	0.09	0.7612
5 vs. 25	20	0.38	0.5376

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.52	0.2188
pre-treatment dens.	20	0.64	0.4226
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.22	0.1365
0 vs. 25	20	0.00	0.9699
5 vs. 25	20	2.28	0.1310

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.16	0.3127
pre-treatment dens.	20	1.03	0.3111
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.39	0.5319
0 vs. 25	20	2.29	0.1301
5 vs. 25	20	0.78	0.3763

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.62	0.0269
pre-treatment dens.	20	0.89	0.3449
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.63	0.0567
0 vs. 25	20	6.74	0.0094
5 vs. 25	20	0.46	0.4978

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.15	0.1167
pre-treatment dens.	20	9.24	0.0024
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.64	0.2004
0 vs. 25	20	0.57	0.4502
5 vs. 25	20	4.21	0.0401

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.40	0.6718
pre-treatment dens.	20	0.56	0.4550
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.07	0.7904
0 vs. 25	20	0.37	0.5441
5 vs. 25	20	0.78	0.3777

mummies

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.42	0.2429
pre-treatment dens.	20	0.85	0.3573
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.05	0.8233
0 vs. 25	20	2.42	0.1196
5 vs. 25	20	1.77	0.1836

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.45	0.0318
pre-treatment dens.	20	0.45	0.5034
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.94	0.1636
0 vs. 25	20	1.43	0.2319
5 vs. 25	20	7.28	0.0070

Syrphid eggs

Drift, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.83	0.4160
aphid dens.	19	11.82	0.0006
pre-treatment dens.	19	0.63	0.4261
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.52	0.4715
0 vs. 25	19	1.26	0.2613
5 vs. 25	19	0.46	0.4975

Control, 19.06.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.16	0.8326
aphid dens.	19	5.59	0.0181
pre-treatment dens.	19	4.25	0.0393
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.28	0.5941
0 vs. 25	19	0.07	0.7885
5 vs. 25	19	0.10	0.7459

Tab. A4 (continued).

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	5.00	0.0067
pre-treatment dens.	20	0.00	0.9911
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	8.50	0.0035
0 vs. 25	20	6.38	0.0115
5 vs. 25	20	0.15	0.6998

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	6.32	0.0018
pre-treatment dens.	20	0.65	0.4186
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	7.87	0.0050
0 vs. 25	20	10.46	0.0012
5 vs. 25	20	0.17	0.6788

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.46	0.6326
pre-treatment dens.	20	2.60	0.1072
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.67	0.4128
0 vs. 25	20	0.71	0.4009
5 vs. 25	20	0.00	0.9825

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.03	0.9666
pre-treatment dens.	20	0.00	0.9958
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9371
0 vs. 25	20	0.03	0.8633
5 vs. 25	20	0.07	0.7939

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.51	0.2201
pre-treatment dens.	20	7.44	0.0064
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9374
0 vs. 25	20	2.39	0.1223
5 vs. 25	20	2.14	0.1435

Drift, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.84	0.4231
aphid dens.	19	6.94	0.0084
pre-treatment dens.	19	0.42	0.5159
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.36	0.5474
0 vs. 25	19	1.42	0.2327
5 vs. 25	19	0.62	0.4315

Control, 26.06.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.13	0.8740
aphid dens.	19	0.38	0.5356
pre-treatment dens.	19	0.21	0.6460
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.02	0.8957
0 vs. 25	19	0.12	0.7330
5 vs. 25	19	0.29	0.5881

Drift, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.19	0.8233
aphid dens.	19	0.09	0.7692
pre-treatment dens.	19	0.00	0.9595
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.38	0.5366
0 vs. 25	19	0.02	0.8879
5 vs. 25	19	0.20	0.6521

Control, 09.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	1.96	0.1410
aphid dens.	19	0.75	0.3879
pre-treatment dens.	19	0.42	0.5160
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.33	0.5662
0 vs. 25	19	3.78	0.0519
5 vs. 25	19	1.75	0.1854

Drift, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.20	0.8174
aphid dens.	19	0.09	0.7614
pre-treatment dens.	19	0.01	0.9216
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.33	0.5654
0 vs. 25	19	0.00	0.9529
5 vs. 25	19	0.29	0.5904

Tab. A4 (continued).

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.13	0.8733
pre-treatment dens.	20	0.10	0.7498
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.00	0.9757
0 vs. 25	20	0.21	0.6451
5 vs. 25	20	0.20	0.6558

Control, 16.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.05	0.9556
aphid dens.	19	0.82	0.3651
pre-treatment dens.	19	0.43	0.5123
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.00	0.9663
0 vs. 25	19	0.08	0.7785
5 vs. 25	19	0.05	0.8165

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.04	0.3523
pre-treatment dens.	20	2.96	0.0851
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9295
0 vs. 25	20	1.45	0.2282
5 vs. 25	20	1.66	0.1970

Drift, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.26	0.7530
aphid dens.	19	4.10	0.0428
pre-treatment dens.	19	0.20	0.6511
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.03	0.8713
0 vs. 25	19	0.23	0.6281
5 vs. 25	19	0.64	0.4240

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.19	0.1120
pre-treatment dens.	20	9.59	0.0020
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.03	0.8536
0 vs. 25	20	3.55	0.0596
5 vs. 25	20	3.10	0.0784

Control, 23.07.02	Type III test of fixed effects		
effect	df	F	p
distance	19	0.00	0.9969
aphid dens.	19	0.34	0.5618
pre-treatment dens.	19	0.13	0.7141
contrasts	AnovaF		
	df	F	p
0 vs. 5	19	0.00	0.9907
0 vs. 25	19	0.01	0.9406
5 vs. 25	19	0.00	0.9535

Sweep net data 2002

Apterous aphids

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	9.05	0.0002
pre-treatment dens.	20	1.24	0.2654
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	10.48	0.0012
0 vs. 24	20	12.41	0.0004
4 vs. 24	20	0.28	0.5982

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	9.76	0.0004
pre-treatment dens.	20	0.58	0.4450
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	5.07	0.0244
0 vs. 24	20	14.36	0.0002
4 vs. 24	20	9.49	0.0021

Alate aphids

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	10.80	<.0001
pre-treatment dens.	20	1.48	0.2231
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	15.77	<.0001
0 vs. 24	20	13.32	0.0003
4 vs. 24	20	0.73	0.3921

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	6.85	0.0011
pre-treatment dens.	20	8.99	0.0027
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	12.81	0.0003
0 vs. 24	20	6.51	0.0107
4 vs. 24	20	1.13	0.2887

Tab. A4 (continued).

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.28	0.0433
pre-treatment dens.	20	0.50	0.4790
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.56	0.0328
0 vs. 24	20	3.82	0.0506
4 vs. 24	20	0.02	0.8760

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.76	0.4612
pre-treatment dens.	20	2.02	0.1555
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.23	0.2669
0 vs. 24	20	0.63	0.4261
4 vs. 24	20	0.23	0.6311

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	14.50	<.0001
pre-treatment dens.	20	0.91	0.3400
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.06	0.0804
0 vs. 24	20	21.09	<.0001
4 vs. 24	20	31.49	<.0001

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.59	0.5546
pre-treatment dens.	20	1.24	0.2653
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.15	0.2839
0 vs. 24	20	0.42	0.5160
4 vs. 24	20	0.19	0.6655

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	11.93	<.0001
pre-treatment dens.	20	7.44	0.0064
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	12.34	0.0004
0 vs. 24	20	17.34	<.0001
4 vs. 24	20	1.08	0.2983

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.00	0.9996
pre-treatment dens.	20	0.00	0.9677
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9904
0 vs. 24	20	0.00	0.9818
4 vs. 24	20	0.00	0.9919

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	10.12	0.0003
pre-treatment dens.	20	4.64	0.0312
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	8.90	0.0029
0 vs. 24	20	13.43	0.0002
4 vs. 24	20	2.05	0.1520

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.20	0.3001
pre-treatment dens.	20	0.13	0.7149
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9904
0 vs. 24	20	0.00	0.9818
4 vs. 24	20	0.00	0.9919

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.71	0.1845
pre-treatment dens.	20	3.76	0.0524
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.33	0.1268
0 vs. 24	20	2.04	0.1534
4 vs. 24	20	0.01	0.9430

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.94	0.0551
pre-treatment dens.	20	1.04	0.3077
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.87	0.0273
0 vs. 24	20	1.87	0.1715
4 vs. 24	20	1.40	0.2364

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.81	0.4067
pre-treatment dens.	20	0.80	0.3707
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.21	0.2719
0 vs. 24	20	0.50	0.4788
4 vs. 24	20	0.52	0.4688

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.48	0.6215
pre-treatment dens.	20	0.01	0.9135
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.12	0.7262
0 vs. 24	20	0.93	0.3339
4 vs. 24	20	0.38	0.5394

Tab. A4 (continued).

Aphid parasitoids				***A. picipes***			
Drift, 20.06.02	Type III test of fixed effects			Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	2.80	0.0590	distance	20	1.01	0.3643
pre-treatment dens.	20	7.70	0.0050	pre-treatment dens.	20	1.99	0.1582
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	4.66	0.0308	0 vs. 4	20	1.78	0.1818
0 vs. 24	20	3.49	0.0619	0 vs. 24	20	0.71	0.4003
4 vs. 24	20	0.23	0.6316	4 vs. 24	20	0.39	0.5330
Control, 20.06.02	Type III test of fixed effects			Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	1.00	0.3590	distance	20	0.23	0.7906
pre-treatment dens.	20	8.90	0.0020	pre-treatment dens.	20	0.34	0.5573
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.96	0.3275	0 vs. 4	20	0.45	0.5040
0 vs. 24	20	1.85	0.1741	0 vs. 24	20	0.07	0.7845
4 vs. 24	20	0.16	0.6861	4 vs. 24	20	0.17	0.6770
Drift, 28.06.02	Type III test of fixed effects			Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	0.90	0.3780	distance	20	0.95	0.3847
pre-treatment dens.	20	0.10	0.6750	pre-treatment dens.	20	0.06	0.8128
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.21	0.6494	0 vs. 4	20	1.32	0.2509
0 vs. 24	20	2.08	0.1493	0 vs. 24	20	0.00	0.9627
4 vs. 24	20	0.80	0.3711	4 vs. 24	20	1.42	0.2339
Control, 28.06.02	Type III test of fixed effects			Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	0.20	0.8040	distance	20	1.67	0.1888
pre-treatment dens.	20	0.00	0.9550	pre-treatment dens.	20	0.00	0.9462
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.00	0.9671	0 vs. 4	20	3.21	0.0732
0 vs. 24	20	0.29	0.5925	0 vs. 24	20	0.51	0.4756
4 vs. 24	20	0.38	0.5395	4 vs. 24	20	1.30	0.2549
Drift, 05.07.02	Type III test of fixed effects			Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	0.60	0.5330	distance	20	2.38	0.0932
pre-treatment dens.	20	0.10	0.6620	pre-treatment dens.	20	1.31	0.2517
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.66	0.4171	0 vs. 4	20	4.18	0.0409
0 vs. 24	20	1.23	0.2669	0 vs. 24	20	1.89	0.1687
4 vs. 24	20	0.04	0.8355	4 vs. 24	20	0.76	0.3846
Control, 05.07.02	Type III test of fixed effects			Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	1.30	0.2560	distance	20	4.07	0.0174
pre-treatment dens.	20	1.10	0.2740	pre-treatment dens.	20	0.65	0.4212
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.49	0.4823	0 vs. 4	20	4.72	0.0299
0 vs. 24	20	2.60	0.1067	0 vs. 24	20	6.62	0.0101
4 vs. 24	20	0.94	0.3324	4 vs. 24	20	0.25	0.6184

Tab. A4 (continued).

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.00	0.3400
pre-treatment dens.	20	0.00	0.8460
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.26	0.6105
0 vs. 24	20	0.93	0.3348
4 vs. 24	20	2.09	0.1481

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.21	0.1105
pre-treatment dens.	20	0.54	0.4605
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.14	0.7061
0 vs. 24	20	4.36	0.0369
4 vs. 24	20	2.60	0.1069

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.50	0.2110
pre-treatment dens.	20	0.10	0.7400
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.66	0.1973
0 vs. 24	20	0.13	0.7237
4 vs. 24	20	3.06	0.0804

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.76	0.0639
pre-treatment dens.	20	0.01	0.9062
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.59	0.4426
0 vs. 24	20	4.94	0.0262
4 vs. 24	20	2.62	0.1053

***A. uzbekist*.-gr.**

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.46	0.2314
pre-treatment dens.	20	0.25	0.6161
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.12	0.1455
0 vs. 24	20	2.26	0.1329
4 vs. 24	20	0.00	0.9621

Chrysopid larvae

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.51	0.5956
pre-treatment dens.	20	0.32	0.5688
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.04	0.8378
0 vs. 24	20	0.00	0.9476
4 vs. 24	20	0.02	0.8805

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.60	0.2014
pre-treatment dens.	20	0.31	0.5789
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.69	0.4072
0 vs. 24	20	3.24	0.0718
4 vs. 24	20	0.91	0.3400

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	6.28	0.0019
pre-treatment dens.	20	0.00	1.0000
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.19	0.6669
0 vs. 24	20	4.43	0.0352
4 vs. 24	20	2.93	0.0867

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.41	0.6644
pre-treatment dens.	20	9.57	0.0020
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.08	0.7837
0 vs. 24	20	0.37	0.5433
4 vs. 24	20	0.78	0.3757

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.06	0.3446
pre-treatment dens.	20	1.01	0.3156
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.21	0.2711
0 vs. 24	20	0.05	0.8173
4 vs. 24	20	2.07	0.1499

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.81	0.4460
pre-treatment dens.	20	0.01	0.9163
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.01	0.9226
0 vs. 24	20	1.11	0.2913
4 vs. 24	20	1.30	0.2533

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.18	0.0420
pre-treatment dens.	20	5.63	0.0177
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.99	0.0255
0 vs. 24	20	3.99	0.0459
4 vs. 24	20	0.14	0.7040

Tab. A4 (continued).

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.84	0.4338
pre-treatment dens.	20	0.38	0.5356
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.18	0.6684
0 vs. 24	20	0.71	0.4008
4 vs. 24	20	1.62	0.2028

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.01	0.9932
pre-treatment dens.	20	0.21	0.6497
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9667
0 vs. 24	20	0.01	0.9122
4 vs. 24	20	0.01	0.9409

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.17	0.1145
pre-treatment dens.	20	1.95	0.1629
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.45	0.5018
0 vs. 24	20	4.23	0.0398
4 vs. 24	20	1.86	0.1724

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.24	0.7864
pre-treatment dens.	20	0.06	0.8113
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.32	0.5713
0 vs. 24	20	0.36	0.5467
4 vs. 24	20	0.00	0.9968

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.32	0.7274
pre-treatment dens.	20	0.00	0.9796
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.36	0.5512
0 vs. 24	20	0.57	0.4497
4 vs. 24	20	0.03	0.8723

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.08	0.1255
pre-treatment dens.	20	0.19	0.6666
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.72	0.0536
0 vs. 24	20	1.92	0.1661
4 vs. 24	20	0.35	0.5558

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	7.91	0.0004
pre-treatment dens.	20	0.47	0.4913
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	14.40	0.0001
0 vs. 24	20	0.83	0.3629
4 vs. 24	20	8.37	0.0038

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	2.29	0.1015
pre-treatment dens.	20	0.02	0.8966
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.17	0.0412
0 vs. 24	20	1.14	0.2848
4 vs. 24	20	1.28	0.2582

Syrphid flies

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	10.50	<.0001
pre-treatment dens.	20	0.20	0.6510
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.32	0.0684
0 vs. 24	20	19.10	<.0001
4 vs. 24	20	8.18	0.0042

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	12.60	<.0001
pre-treatment dens.	20	2.20	0.1360
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	7.65	0.0057
0 vs. 24	20	25.44	<.0001
4 vs. 24	20	5.13	0.0235

E. balteatus

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.70	0.1834
pre-treatment dens.	20	1.38	0.2400
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.42	0.5188
0 vs. 24	20	3.16	0.0757
4 vs. 24	20	1.49	0.2218

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.65	0.0261
pre-treatment dens.	20	0.11	0.7365
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.56	0.0592
0 vs. 24	20	7.14	0.0075
4 vs. 24	20	0.48	0.4870

Tab. A4 (continued).

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.20	0.0390
pre-treatment dens.	20	0.00	0.9450
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.19	0.0739
0 vs. 24	20	5.63	0.0177
4 vs. 24	20	0.53	0.4666

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.78	0.4561
pre-treatment dens.	20	2.61	0.1063
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.49	0.2221
0 vs. 24	20	0.37	0.5416
4 vs. 24	20	0.43	0.5097

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	3.90	0.0200
pre-treatment dens.	20	1.10	0.2790
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	5.29	0.0215
0 vs. 24	20	6.54	0.0105
4 vs. 24	20	0.08	0.7772

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.23	0.2914
pre-treatment dens.	20	0.45	0.5047
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9445
0 vs. 24	20	1.83	0.1756
4 vs. 24	20	1.90	0.1682

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	22.90	<.0001
pre-treatment dens.	20	0.00	0.9360
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	20.36	<.0001
0 vs. 24	20	40.52	<.0001
4 vs. 24	20	5.06	0.0245

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	6.39	0.0017
pre-treatment dens.	20	0.54	0.4614
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	9.14	0.0025
0 vs. 24	20	9.14	0.0025
4 vs. 24	20	0.00	1.0000

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	43.80	<.0001
pre-treatment dens.	20	0.00	0.9530
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	38.93	<.0001
0 vs. 24	20	85.09	<.0001
4 vs. 24	20	9.02	0.0027

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	14.72	<.0001
pre-treatment dens.	20	0.84	0.3603
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	11.59	0.0007
0 vs. 24	20	30.02	<.0001
4 vs. 24	20	3.57	0.0588

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	45.70	<.0001
pre-treatment dens.	20	0.10	0.7180
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	30.03	<.0001
0 vs. 24	20	83.38	<.0001
4 vs. 24	20	18.07	<.0001

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	9.33	<.0001
pre-treatment dens.	20	0.00	0.9661
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	12.97	0.0003
0 vs. 24	20	13.68	0.0002
4 vs. 24	20	0.01	0.9172

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	19.60	<.0001
pre-treatment dens.	20	0.00	0.7640
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	21.40	<.0001
0 vs. 24	20	36.40	<.0001
4 vs. 24	20	2.07	0.1505

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	61.42	<.0001
pre-treatment dens.	20	0.00	1.0000
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	97.87	<.0001
0 vs. 24	20	87.36	<.0001
4 vs. 24	20	0.75	0.3879

Tab. A4 (continued).

M. mellinum

Drift, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.02	0.3607
pre-treatment dens.	20	8.01	0.0046
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.36	0.5465
0 vs. 24	20	2.12	0.1453
4 vs. 24	20	0.65	0.4214

Drift, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.91	0.4036
pre-treatment dens.	20	0.22	0.6426
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.32	0.2509
0 vs. 24	20	1.44	0.2306
4 vs. 24	20	0.00	0.9920

Control, 20.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	1.91	0.1475
pre-treatment dens.	20	2.83	0.0927
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.16	0.6910
0 vs. 24	20	3.44	0.0637
4 vs. 24	20	2.13	0.1446

Control, 28.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	0.72	0.4861
pre-treatment dens.	20	6.59	0.0103
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.45	0.2291
0 vs. 24	20	0.28	0.5962
4 vs. 24	20	0.44	0.5051

Drift, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	31.09	<.0001
pre-treatment dens.	20	0.46	0.4999
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	21.32	<.0001
0 vs. 24	20	64.36	<.0001
4 vs. 24	20	9.82	0.0017

Drift, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	41.78	<.0001
pre-treatment dens.	20	0.33	0.5656
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	19.51	<.0001
0 vs. 24	20	87.52	<.0001
4 vs. 24	20	21.35	<.0001

Control, 05.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	23.43	<.0001
pre-treatment dens.	20	1.20	0.2737
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	25.03	<.0001
0 vs. 24	20	42.83	<.0001
4 vs. 24	20	2.46	0.1169

Control, 12.07.02	Type III test of fixed effects		
effect	df	F	p
distance	20	15.84	<.0001
pre-treatment dens.	20	0.20	0.6568
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	16.89	<.0001
0 vs. 24	20	28.97	<.0001
4 vs. 24	20	1.68	0.1953

Tab. A4 (continued).

Count data 2003

Cereal aphids

Drift, 23.06.02	Type III test of fixed effects		
effect	df	F	p
distance	20	4.52	0.0118
pre-treatment dens.	20	0.03	0.8730
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	5.69	0.0170
0 vs. 25	20	6.95	0.0084
5 vs. 25	20	0.00	0.9823

Control, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	26.62	<.0001
pre-treatment dens.	20	1.16	0.2806
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	22.15	<.0001
0 vs. 25	20	48.58	<.0001
5 vs. 25	20	6.09	0.0136

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.74	0.0254
pre-treatment dens.	20	0.34	0.5578
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.70	0.1002
0 vs. 25	20	7.33	0.0068
5 vs. 25	20	0.96	0.3261

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.24	0.1067
pre-treatment dens.	20	1.69	0.1930
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.16	0.0413
0 vs. 25	20	1.74	0.1870
5 vs. 25	20	0.60	0.4397

Drift, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.13	0.8694
pre-treatment dens.	20	0.29	0.5885
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.16	0.6884
0 vs. 25	20	0.21	0.6498
5 vs. 25	20	0.00	0.9876

Control, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.81	0.4435
pre-treatment dens.	20	0.07	0.7847
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.27	0.6051
0 vs. 25	20	1.52	0.2170
5 vs. 25	20	0.61	0.4361

R. padi

Drift, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.69	0.0017
pre-treatment dens.	20	0.14	0.7044
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	9.46	0.0021
0 vs. 25	20	8.07	0.0045
5 vs. 25	20	0.14	0.7127

Control, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	9.70	<.0001
pre-treatment dens.	20	0.78	0.3766
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	6.94	0.0084
0 vs. 25	20	17.66	<.0001
5 vs. 25	20	3.09	0.0789

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.50	0.0051
pre-treatment dens.	20	0.23	0.6315
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	5.66	0.0173
0 vs. 25	20	8.66	0.0033
5 vs. 25	20	0.40	0.5247

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	8.65	0.0002
pre-treatment dens.	20	0.04	0.8426
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	11.79	0.0006
0 vs. 25	20	12.23	0.0005
5 vs. 25	20	0.00	0.9606

Drift, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	8.18	0.0004
pre-treatment dens.	20	0.02	0.9001
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	10.11	0.0015
0 vs. 25	20	11.49	0.0007
5 vs. 25	20	0.03	0.8576

Control, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.68	0.0037
pre-treatment dens.	20	0.14	0.7093
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	3.81	0.0510
0 vs. 25	20	10.42	0.0012
5 vs. 25	20	2.04	0.1527

Tab. A4 (continued).

Drift, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.57	0.2085
pre-treatment dens.	20	0.53	0.4657
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.12	0.1450
0 vs. 25	20	2.23	0.1354
5 vs. 25	20	0.01	0.9094

Drift, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.29	0.7320
pre-treatment dens.	20	0.91	0.3394
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.03	0.8549
0 vs. 25	20	0.26	0.6095
5 vs. 25	20	0.75	0.3880

Control, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.21	0.2971
pre-treatment dens.	20	0.25	0.6163
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.20	0.6555
0 vs. 25	20	2.19	0.1393
5 vs. 25	20	1.25	0.2630

Control, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.44	0.2377
pre-treatment dens.	20	0.03	0.8550
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.08	0.2981
0 vs. 25	20	2.60	0.1069
5 vs. 25	20	0.41	0.5222

Drift, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.39	0.6669
pre-treatment dens.	20	0.03	0.8718
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.65	0.4208
0 vs. 25	20	0.10	0.7476
5 vs. 25	20	0.37	0.5423

Drift, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.06	0.9352
pre-treatment dens.	20	0.03	0.8636
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.06	0.8071
0 vs. 25	20	0.00	0.9620
5 vs. 25	20	0.13	0.7134

Control, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.17	0.8404
pre-treatment dens.	20	0.81	0.3693
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.16	0.6901
0 vs. 25	20	0.31	0.5803
5 vs. 25	20	0.03	0.8662

Control, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.90	0.1502
pre-treatment dens.	20	1.47	0.2249
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.46	0.4981
0 vs. 25	20	3.46	0.0628
5 vs. 25	20	1.78	0.1823

S. avenae

Drift, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.87	0.1559
pre-treatment dens.	20	1.34	0.2470
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.39	0.2379
0 vs. 25	20	3.09	0.0786
5 vs. 25	20	0.74	0.3896

Control, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.64	0.0013
pre-treatment dens.	20	0.92	0.3380
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	7.79	0.0053
0 vs. 25	20	11.68	0.0006
5 vs. 25	20	0.29	0.5893

M. dirhodum

Drift, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.53	0.2160
pre-treatment dens.	20	0.64	0.4223
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.31	0.1282
0 vs. 25	20	2.42	0.1196
5 vs. 25	20	0.03	0.8648

Control, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.95	0.3879
pre-treatment dens.	20	0.05	0.8282
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9340
0 vs. 25	20	1.54	0.2146
5 vs. 25	20	1.28	0.2586

Tab. A4 (continued).

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	11.06	<.0001
pre-treatment dens.	20	1.52	0.2181
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	7.82	0.0052
0 vs. 25	20	18.35	<.0001
5 vs. 25	20	4.71	0.0300

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.24	0.0055
pre-treatment dens.	20	3.37	0.0662
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	7.30	0.0069
0 vs. 25	20	8.65	0.0033
5 vs. 25	20	0.23	0.6331

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.60	0.0037
pre-treatment dens.	20	9.85	0.0017
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	9.94	0.0016
0 vs. 25	20	5.81	0.0159
5 vs. 25	20	0.72	0.3963

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.36	0.0047
pre-treatment dens.	20	0.09	0.7630
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	7.20	0.0073
0 vs. 25	20	9.05	0.0026
5 vs. 25	20	0.10	0.7516

Drift, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.22	0.1107
pre-treatment dens.	20	0.30	0.5833
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.24	0.0395
0 vs. 25	20	2.48	0.1150
5 vs. 25	20	0.04	0.8513

Drift, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.90	0.0560
pre-treatment dens.	20	0.08	0.7794
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.95	0.0260
0 vs. 25	20	4.16	0.0415
5 vs. 25	20	0.00	0.9894

Control, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.12	0.0444
pre-treatment dens.	20	2.57	0.1089
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	5.90	0.0151
0 vs. 25	20	2.16	0.1418
5 vs. 25	20	1.09	0.2966

Control, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	17.36	<.0001
pre-treatment dens.	20	0.42	0.5172
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	29.65	<.0001
0 vs. 25	20	22.87	<.0001
5 vs. 25	20	0.42	0.5179

Drift, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.93	0.1469
pre-treatment dens.	20	1.25	0.2626
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.14	0.7069
0 vs. 25	20	2.85	0.0916
5 vs. 25	20	2.40	0.1212

Drift, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.55	0.0041
pre-treatment dens.	20	1.15	0.2836
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	9.73	0.0018
0 vs. 25	20	7.76	0.0054
5 vs. 25	20	0.00	0.9570

Control, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.33	0.7195
pre-treatment dens.	20	1.23	0.2674
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.41	0.5236
0 vs. 25	20	0.01	0.9274
5 vs. 25	20	0.57	0.4510

Control, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	8.62	0.0002
pre-treatment dens.	20	3.12	0.0773
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	16.79	<.0001
0 vs. 25	20	7.84	0.0051
5 vs. 25	20	1.60	0.2055

Tab. A4 (continued).

Drift, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.38	0.0948
pre-treatment dens.	20	1.56	0.2114
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.27	0.0389
0 vs. 25	20	2.89	0.0892
5 vs. 25	20	0.00	0.9562

Drift, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.91	0.3995
pre-treatment dens.	20	1.59	0.2075
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.01	0.1561
0 vs. 25	20	0.77	0.3814
5 vs. 25	20	0.17	0.6809

Control, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.07	0.9366
pre-treatment dens.	20	0.29	0.5887
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.01	0.9095
0 vs. 25	20	0.06	0.8104
5 vs. 25	20	0.13	0.7193

Control, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.66	0.5157
pre-treatment dens.	20	0.33	0.5658
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.27	0.2593
0 vs. 25	20	0.64	0.4240
5 vs. 25	20	0.10	0.7487

Chrysopid eggs

Drift, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	23.95	<.0001
pre-treatment dens.	20	0.78	0.3763
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	23.05	<.0001
0 vs. 25	20	46.12	<.0001
5 vs. 25	20	3.10	0.0783

Chrysopid eggs

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.91	0.1479
pre-treatment dens.	20	0.12	0.7316
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	1.81	0.1787
0 vs. 25	20	3.70	0.0544
5 vs. 25	20	0.26	0.6071

Control, 23.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.66	0.5181
pre-treatment dens.	20	0.26	0.6106
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.62	0.4317
0 vs. 25	20	1.18	0.2783
5 vs. 25	20	0.11	0.7366

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.61	0.2005
pre-treatment dens.	20	0.47	0.4940
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.88	0.0897
0 vs. 25	20	1.70	0.1918
5 vs. 25	20	0.14	0.7104

Drift, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.85	0.0078
pre-treatment dens.	20	0.03	0.8584
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	4.30	0.0380
0 vs. 25	20	9.54	0.0020
5 vs. 25	20	0.84	0.3608

Drift, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	16.79	<.0001
pre-treatment dens.	20	0.71	0.3995
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	25.05	<.0001
0 vs. 25	20	24.76	<.0001
5 vs. 25	20	0.06	0.8018

Control, 07.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	17.24	<.0001
pre-treatment dens.	20	0.00	0.9957
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	10.91	0.0010
0 vs. 25	20	32.46	<.0001
5 vs. 25	20	6.89	0.0087

Control, 14.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.20	0.1106
pre-treatment dens.	20	2.82	0.0933
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	2.91	0.0878
0 vs. 25	20	3.45	0.0632
5 vs. 25	20	0.04	0.8381

Tab. A4 (continued).

Drift, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	14.04	<.0001
pre-treatment dens.	20	0.50	0.4779
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	5.01	0.0253
0 vs. 25	20	28.93	<.0001
5 vs. 25	20	9.10	0.0026

Control, 21.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.17	0.0421
pre-treatment dens.	20	1.66	0.1976
contrasts	AnovaF		
	df	F	p
0 vs. 5	20	0.98	0.3213
0 vs. 25	20	2.15	0.1423
5 vs. 25	20	6.67	0.0098

Sweep net data 2003

Apterous aphids

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.96	0.0020
pre-treatment dens.	20	0.78	0.3768
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	7.50	0.0062
0 vs. 24	20	9.36	0.0022
4 vs. 24	20	0.25	0.6191

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.10	0.0094
pre-treatment dens.	20	2.97	0.0851
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.85	0.0277
0 vs. 24	20	7.53	0.0061
4 vs. 24	20	0.53	0.4647

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	7.99	0.0008
pre-treatment dens.	20	0.34	0.5603
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	9.09	0.0026
0 vs. 24	20	10.34	0.0013
4 vs. 24	20	0.10	0.7521

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.44	0.0029
pre-treatment dens.	20	3.47	0.0625
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.62	0.0571
0 vs. 24	20	10.66	0.0011
4 vs. 24	20	3.72	0.0536

Alate aphids

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.14	0.3181
pre-treatment dens.	20	0.10	0.7493
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.19	0.1393
0 vs. 24	20	0.62	0.4300
4 vs. 24	20	0.55	0.4589

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.80	0.0092
pre-treatment dens.	20	6.33	0.0118
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.31	0.0687
0 vs. 24	20	7.91	0.0049
4 vs. 24	20	2.01	0.1558

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.27	0.0141
pre-treatment dens.	20	1.97	0.1609
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.73	0.0533
0 vs. 24	20	7.98	0.0047
4 vs. 24	20	0.82	0.3650

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.04	0.3494
pre-treatment dens.	20	18.64	<.0001
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.98	0.1589
0 vs. 24	20	0.10	0.7559
4 vs. 24	20	1.32	0.2507

Tab. A4 (continued).

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.95	0.0112
pre-treatment dens.	20	0.73	0.3924
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	5.45	0.0196
0 vs. 24	20	6.56	0.0104
4 vs. 24	20	0.12	0.7256

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.22	0.0149
pre-treatment dens.	20	0.22	0.6377
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	6.04	0.0139
0 vs. 24	20	6.20	0.0128
4 vs. 24	20	0.00	0.9994

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.99	0.3613
pre-treatment dens.	20	0.46	0.4971
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.35	0.5519
0 vs. 24	20	1.65	0.1993
4 vs. 24	20	0.97	0.3248

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.18	0.8295
pre-treatment dens.	20	12.16	0.0005
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.36	0.5476
0 vs. 24	20	0.07	0.7961
4 vs. 24	20	0.11	0.7347

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.33	0.6782
pre-treatment dens.	20	1.35	0.2447
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.10	0.7479
0 vs. 24	20	0.53	0.4670
4 vs. 24	20	0.38	0.5382

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	7.57	0.0005
pre-treatment dens.	20	0.69	0.4073
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	9.44	0.0021
0 vs. 24	20	12.40	0.0004
4 vs. 24	20	0.18	0.6697

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.23	0.7552
pre-treatment dens.	20	0.00	0.9958
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9853
0 vs. 24	20	0.30	0.5841
4 vs. 24	20	0.59	0.4426

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.08	0.0483
pre-treatment dens.	20	11.52	0.0007
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.10	0.0428
0 vs. 24	20	4.31	0.0378
4 vs. 24	20	0.10	0.7553

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.84	0.4107
pre-treatment dens.	20	0.29	0.5910
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.49	0.4833
0 vs. 24	20	1.35	0.2455
4 vs. 24	20	0.49	0.4842

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.14	0.8698
pre-treatment dens.	20	0.04	0.8403
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.13	0.7146
0 vs. 24	20	0.02	0.8950
4 vs. 24	20	0.28	0.5994

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.09	0.8848
pre-treatment dens.	20	0.06	0.8046
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.01	0.9176
0 vs. 24	20	0.14	0.7090
4 vs. 24	20	0.15	0.6972

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.40	0.6613
pre-treatment dens.	20	4.19	0.0407
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.37	0.5415
0 vs. 24	20	0.63	0.4259
4 vs. 24	20	0.09	0.7650

Tab. A4 (continued).

Syrphid flies

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	16.30	<.0001
pre-treatment dens.	20	0.02	0.8915
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	17.31	<.0001
0 vs. 24	20	25.23	<.0001
4 vs. 24	20	1.36	0.2439

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	38.77	<.0001
pre-treatment dens.	20	0.02	0.8955
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	30.89	<.0001
0 vs. 24	20	69.58	<.0001
4 vs. 24	20	10.38	0.0013

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	33.32	<.0001
pre-treatment dens.	20	0.79	0.3742
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	25.04	<.0001
0 vs. 24	20	56.49	<.0001
4 vs. 24	20	10.32	0.0013

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	18.42	<.0001
pre-treatment dens.	20	0.19	0.6663
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	13.71	0.0002
0 vs. 24	20	33.36	<.0001
4 vs. 24	20	5.70	0.0170

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	15.78	<.0001
pre-treatment dens.	20	0.64	0.4250
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.18	0.0746
0 vs. 24	20	26.66	<.0001
4 vs. 24	20	17.62	<.0001

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	28.68	<.0001
pre-treatment dens.	20	0.49	0.4817
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	17.21	<.0001
0 vs. 24	20	52.79	<.0001
4 vs. 24	20	12.61	0.0004

E. balteatus

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	26.54	<.0001
pre-treatment dens.	20	0.14	0.7090
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	36.39	<.0001
0 vs. 24	20	39.82	<.0001
4 vs. 24	20	0.38	0.5366

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	21.75	<.0001
pre-treatment dens.	20	0.09	0.7671
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	20.98	<.0001
0 vs. 24	20	41.69	<.0001
4 vs. 24	20	2.67	0.1026

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	20.44	<.0001
pre-treatment dens.	20	0.30	0.5853
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	14.12	0.0002
0 vs. 24	20	37.17	<.0001
4 vs. 24	20	7.48	0.0062

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	9.29	<.0001
pre-treatment dens.	20	3.41	0.0648
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.07	0.1498
0 vs. 24	20	18.71	<.0001
4 vs. 24	20	7.89	0.0050

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	9.15	0.0001
pre-treatment dens.	20	0.09	0.7694
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.13	0.2887
0 vs. 24	20	15.57	<.0001
4 vs. 24	20	10.15	0.0014

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	15.36	<.0001
pre-treatment dens.	20	0.09	0.7635
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.41	0.1203
0 vs. 24	20	30.19	<.0001
4 vs. 24	20	14.88	0.0001

Tab. A4 (continued).

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	13.62	<.0001
pre-treatment dens.	20	1.97	0.1607
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	9.35	0.0022
0 vs. 24	20	23.36	<.0001
4 vs. 24	20	5.10	0.0239

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.98	0.0513
pre-treatment dens.	20	0.55	0.4579
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.07	0.7971
0 vs. 24	20	3.58	0.0584
4 vs. 24	20	5.38	0.0204

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	10.11	<.0001
pre-treatment dens.	20	0.12	0.7244
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.58	0.0324
0 vs. 24	20	18.69	<.0001
4 vs. 24	20	6.09	0.0136

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.05	0.1284
pre-treatment dens.	20	0.54	0.4624
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.30	0.5851
0 vs. 24	20	4.02	0.0451
4 vs. 24	20	2.04	0.1530

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	45.40	<.0001
pre-treatment dens.	20	0.01	0.9203
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	51.78	<.0001
0 vs. 24	20	67.94	<.0001
4 vs. 24	20	2.16	0.1418

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	-	-
pre-treatment dens.	20	-	-
contrasts	AnovaF		
	df	F	p
0 vs. 4	-	-	-
0 vs. 24	-	-	-
4 vs. 24	-	-	-

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	36.82	<.0001
pre-treatment dens.	20	1.17	0.2804
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	36.83	<.0001
0 vs. 24	20	63.00	<.0001
4 vs. 24	20	4.95	0.0261

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.04	0.1300
pre-treatment dens.	20	30.4	0.0811
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.34	0.0676
0 vs. 24	20	2.53	0.1114
4 vs. 24	20	0.11	0.7394

M. mellinum

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.37	0.2537
pre-treatment dens.	20	0.68	0.4095
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.98	0.3227
0 vs. 24	20	2.70	0.1007
4 vs. 24	20	0.43	0.5114

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.11	0.0022
pre-treatment dens.	20	0.12	0.7275
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	11.59	0.0007
0 vs. 24	20	6.60	0.0102
4 vs. 24	20	0.52	0.4717

S. scripta

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.24	0.7663
pre-treatment dens.	20	6.92	0.0085
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.32	0.5746
0 vs. 24	20	0.32	0.5746
4 vs. 24	20	0.00	1.0000

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.56	0.0843
pre-treatment dens.	20	0.00	0.9677
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.32	0.1281
0 vs. 24	20	3.97	0.0463
4 vs. 24	20	0.41	0.5238

Tab. A4 (continued).

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	7.44	0.0006
pre-treatment dens.	20	2.81	0.0935
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.07	0.1498
0 vs. 24	20	14.53	0.0001
4 vs. 24	20	5.69	0.0170

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	12.37	<.0001
pre-treatment dens.	20	1.47	0.2248
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	16.13	<.0001
0 vs. 24	20	16.13	<.0001
4 vs. 24	20	0.00	1.0000

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.15	0.0429
pre-treatment dens.	20	0.25	0.6182
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.40	0.0359
0 vs. 24	20	5.08	0.0242
4 vs. 24	20	0.05	0.8198

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	43.92	<.0001
pre-treatment dens.	20	31.19	<.0001
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	55.90	<.0001
0 vs. 24	20	55.90	<.0001
4 vs. 24	20	0.00	1.0000

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.65	0.5230
pre-treatment dens.	20	0.20	0.6564
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.11	0.7392
0 vs. 24	20	1.23	0.2682
4 vs. 24	20	0.61	0.4360

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.19	0.0178
pre-treatment dens.	20	0.22	0.6410
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.02	0.1556
0 vs. 24	20	7.28	0.0070
4 vs. 24	20	2.69	0.1012

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.18	0.0418
pre-treatment dens.	20	0.84	0.3582
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	5.19	0.0227
0 vs. 24	20	4.47	0.0345
4 vs. 24	20	0.01	0.9305

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	20.53	<.0001
pre-treatment dens.	20	2.24	0.1342
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	26.13	<.0001
0 vs. 24	20	26.13	<.0001
4 vs. 24	20	0.00	1.0000

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.29	0.0374
pre-treatment dens.	20	0.32	0.5695
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9508
0 vs. 24	20	5.05	0.0247
4 vs. 24	20	4.83	0.0280

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	9.48	0.0001
pre-treatment dens.	20	0.47	0.4940
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	12.37	0.0004
0 vs. 24	20	12.37	0.0004
4 vs. 24	20	0.00	1.0000

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.23	0.0146
pre-treatment dens.	20	0.05	0.8300
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	20	0.5110
0 vs. 24	20	20	0.0124
4 vs. 24	20	20	0.0483

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	18.95	<.0001
pre-treatment dens.	20	5.50	0.0191
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	21.11	<.0001
0 vs. 24	20	26.78	<.0001
4 vs. 24	20	0.62	0.4325

Tab. A4 (continued).

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	22.32	<.0001
pre-treatment dens.	20	0.09	0.7645
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	28.97	<.0001
0 vs. 24	20	37.22	<.0001
4 vs. 24	20	0.52	0.4700

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	43.56	<.0001
pre-treatment dens.	20	0.12	0.7247
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	50.89	<.0001
0 vs. 24	20	62.17	<.0001
4 vs. 24	20	0.93	0.3356

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	9.15	0.0001
pre-treatment dens.	20	0.00	1.0000
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	11.43	0.0007
0 vs. 24	20	15.68	<.0001
4 vs. 24	20	0.48	0.4877

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.79	0.0110
pre-treatment dens.	20	0.23	0.6295
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.86	0.0493
0 vs. 24	20	7.68	0.0056
4 vs. 24	20	1.19	0.2751

E. corollae

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.71	0.0012
pre-treatment dens.	20	6.71	0.0012
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	7.01	0.0081
0 vs. 24	20	12.37	0.0004
4 vs. 24	20	0.76	0.3838

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	21.43	<.0001
pre-treatment dens.	20	21.43	<.0001
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	18.96	<.0001
0 vs. 24	20	41.10	<.0001
4 vs. 24	20	4.23	0.0397

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.16	0.0021
pre-treatment dens.	20	6.16	0.0021
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	10.84	0.0010
0 vs. 24	20	7.27	0.0070
4 vs. 24	20	0.36	0.5510

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.96	0.0070
pre-treatment dens.	20	4.96	0.0070
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.42	0.0354
0 vs. 24	20	9.50	0.0021
4 vs. 24	20	0.96	0.3277

Aphid parasitoids

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.79	0.0618
pre-treatment dens.	20	0.79	0.3749
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.47	0.4919
0 vs. 24	20	5.03	0.0249
4 vs. 24	20	2.57	0.1091

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.20	0.8220
pre-treatment dens.	20	0.00	0.9680
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.35	0.5532
0 vs. 24	20	0.01	0.9073
4 vs. 24	20	0.22	0.6374

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.54	0.0794
pre-treatment dens.	20	0.37	0.5406
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.03	0.8540
0 vs. 24	20	3.30	0.0692
4 vs. 24	20	3.96	0.0467

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.54	0.0794
pre-treatment dens.	20	0.37	0.5406
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9623
0 vs. 24	20	0.05	0.8280
4 vs. 24	20	0.03	0.8666

Tab. A4 (continued).

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.41	0.0329
pre-treatment dens.	20	3.41	0.0329
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.28	0.2582
0 vs. 24	20	6.79	0.0092
4 vs. 24	20	2.17	0.1403

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.62	0.0733
pre-treatment dens.	20	0.46	0.4966
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.83	0.0279
0 vs. 24	20	3.26	0.0712
4 vs. 24	20	0.06	0.8060

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.61	0.0099
pre-treatment dens.	20	4.61	0.0099
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	8.21	0.0042
0 vs. 24	20	5.31	0.0212
4 vs. 24	20	0.32	0.5741

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.62	0.0733
pre-treatment dens.	20	0.46	0.4966
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.13	0.7189
0 vs. 24	20	2.23	0.1355
4 vs. 24	20	1.26	0.2625

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.08	0.0169
pre-treatment dens.	20	4.08	0.0169
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.38	0.0365
0 vs. 24	20	7.46	0.0063
4 vs. 24	20	0.41	0.5227

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.62	0.0100
pre-treatment dens.	20	0.45	0.5045
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.79	0.3748
0 vs. 24	20	8.34	0.0039
4 vs. 24	20	4.24	0.0394

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	11.38	<.0001
pre-treatment dens.	20	11.38	<.0001
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	17.07	<.0001
0 vs. 24	20	17.07	<.0001
4 vs. 24	20	0.00	1.0000

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.32	0.0133
pre-treatment dens.	20	0.21	0.6494
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	7.41	0.0065
0 vs. 24	20	5.51	0.0189
4 vs. 24	20	0.14	0.7109

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.14	0.0158
pre-treatment dens.	20	4.14	0.0158
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	6.22	0.0127
0 vs. 24	20	6.22	0.0127
4 vs. 24	20	0.00	1.0000

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.22	0.8018
pre-treatment dens.	20	6.19	0.0129
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.13	0.7137
0 vs. 24	20	0.09	0.7609
4 vs. 24	20	0.42	0.5180

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	11.59	<.0001
pre-treatment dens.	20	11.59	<.0001
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	14.15	0.0002
0 vs. 24	20	20.09	<.0001
4 vs. 24	20	0.52	0.4713

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.49	0.6152
pre-treatment dens.	20	0.13	0.7231
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.31	0.5750
0 vs. 24	20	0.18	0.6705
4 vs. 24	20	0.95	0.3294

Tab. A4 (continued).

***A. uzbek*.-gr.**				**Adult chrysopids**			
Drift, 24.06.03	Type III test of fixed effects			Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	2.79	0.0618	distance	20	3.96	0.0193
pre-treatment dens.	20	0.79	0.3749	pre-treatment dens.	20	1.30	0.2543
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.47	0.4919	0 vs. 4	20	4.93	0.0264
0 vs. 24	20	5.03	0.0249	0 vs. 24	20	7.22	0.0072
4 vs. 24	20	2.57	0.1091	4 vs. 24	20	0.18	0.6730
Control, 24.06.03	Type III test of fixed effects			Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	0.48	0.6185	distance	20	0.59	0.5541
pre-treatment dens.	20	2.87	0.0904	pre-treatment dens.	20	0.04	0.8429
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.00	0.9768	0 vs. 4	20	1.04	0.3075
0 vs. 24	20	0.76	0.3823	0 vs. 24	20	0.82	0.3665
4 vs. 24	20	0.71	0.3989	4 vs. 24	20	0.01	0.9299
Drift, 30.06.03	Type III test of fixed effects			Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	1.13	0.3231	distance	20	1.17	0.0311
pre-treatment dens.	20	0.58	0.4459	pre-treatment dens.	20	1.52	0.2170
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.25	0.6174	0 vs. 4	20	0.00	0.9588
0 vs. 24	20	2.07	0.1499	0 vs. 24	20	1.76	0.1846
4 vs. 24	20	0.95	0.3300	4 vs. 24	20	1.69	0.1933
Control, 30.06.03	Type III test of fixed effects			Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	0.71	0.4890	distance	20	1.55	0.2115
pre-treatment dens.	20	0.60	0.4368	pre-treatment dens.	20	0.02	0.9012
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.30	0.5829	0 vs. 4	20	0.81	0.3694
0 vs. 24	20	1.46	0.2263	0 vs. 24	20	0.84	0.3602
4 vs. 24	20	0.41	0.5221	4 vs. 24	20	2.81	0.0938
Drift, 08.07.03	Type III test of fixed effects			Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	1.49	0.2258	distance	20	2.88	0.0565
pre-treatment dens.	20	2.27	0.1316	pre-treatment dens.	20	0.94	0.3317
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	3.01	0.0825	0 vs. 4	20	2.17	0.1407
0 vs. 24	20	1.49	0.2218	0 vs. 24	20	5.93	0.0149
4 vs. 24	20	0.16	0.6911	4 vs. 24	20	0.80	0.3702
Control, 08.07.03	Type III test of fixed effects			Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p	effect	df	F	p
distance	20	3.10	0.0453	distance	20	0.74	0.4762
pre-treatment dens.	20	0.00	0.9643	pre-treatment dens.	20	1.72	0.1899
contrasts	AnovaF			contrasts	AnovaF		
	df	F	p		df	F	p
0 vs. 4	20	0.04	0.8504	0 vs. 4	20	1.36	0.2430
0 vs. 24	20	5.17	0.0230	0 vs. 24	20	0.03	0.8726
4 vs. 24	20	4.32	0.0377	4 vs. 24	20	0.84	0.3593

Tab. A4 (continued).

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.19	0.0154
pre-treatment dens.	20	0.72	0.3953
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.94	0.3329
0 vs. 24	20	7.70	0.0055
4 vs. 24	20	3.50	0.0612

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.45	0.0864
pre-treatment dens.	20	1.77	0.1837
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.05	0.0442
0 vs. 24	20	3.56	0.0591
4 vs. 24	20	0.02	0.8933

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.27	0.0381
pre-treatment dens.	20	0.00	0.9945
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.03	0.0448
0 vs. 24	20	5.64	0.0175
4 vs. 24	20	0.09	0.7695

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.05	0.9496
pre-treatment dens.	20	0.76	0.3839
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.08	0.7775
0 vs. 24	20	0.08	0.7785
4 vs. 24	20	0.00	0.9962

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.47	0.2295
pre-treatment dens.	20	3.64	0.0565
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.45	0.1176
0 vs. 24	20	2.10	0.1478
4 vs. 24	20	0.00	0.9907

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.03	0.7763
pre-treatment dens.	20	0.13	0.7232
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.03	0.8619
0 vs. 24	20	0.49	0.4854
4 vs. 24	20	0.24	0.6222

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.80	0.1652
pre-treatment dens.	20	0.66	0.4162
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.50	0.2211
0 vs. 24	20	3.55	0.0595
4 vs. 24	20	0.38	0.5387

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.07	0.9313
pre-treatment dens.	20	1.62	0.2030
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.12	0.7319
0 vs. 24	20	0.10	0.7489
4 vs. 24	20	0.00	0.9891

Chrysopid larvae

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.60	0.5505
pre-treatment dens.	20	0.19	0.6603
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.04	0.8490
0 vs. 24	20	1.07	0.3004
4 vs. 24	20	0.67	0.4138

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.87	0.1538
pre-treatment dens.	20	0.24	0.6240
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.42	0.5161
0 vs. 24	20	3.58	0.0586
4 vs. 24	20	1.59	0.2078

Coccinellidae

Drift, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.31	0.7055
pre-treatment dens.	20	5.62	0.0177
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.46	0.4977
0 vs. 24	20	0.30	0.5854
4 vs. 24	20	0.05	0.8276

Control, 24.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	5.36	0.0062
pre-treatment dens.	20	6.09	0.0136
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	7.11	0.0077
0 vs. 24	20	6.71	0.0096
4 vs. 24	20	0.10	0.7521

Tab. A4 (continued).

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.81	0.1637
pre-treatment dens.	20	3.38	0.0659
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	3.58	0.0586
0 vs. 24	20	1.65	0.1986
4 vs. 24	20	0.33	0.5658

Drift, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.96	0.3747
pre-treatment dens.	20	1.22	0.2694
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.08	0.2981
0 vs. 24	20	1.36	0.2436
4 vs. 24	20	0.01	0.9192

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	4.33	0.0132
pre-treatment dens.	20	0.90	0.3438
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.18	0.1399
0 vs. 24	20	8.55	0.0034
4 vs. 24	20	2.18	0.1399

Control, 30.06.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.64	0.1957
pre-treatment dens.	20	2.64	0.1041
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.19	0.2758
0 vs. 24	20	2.91	0.0880
4 vs. 24	20	0.47	0.4941

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	1.17	0.3091
pre-treatment dens.	20	1.95	0.1626
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.06	0.3031
0 vs. 24	20	2.30	0.1293
4 vs. 24	20	0.23	0.6338

Drift, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.01	0.9884
pre-treatment dens.	20	1.59	0.2076
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9879
0 vs. 24	20	0.01	0.9177
4 vs. 24	20	0.01	0.9078

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	21.81	<.0001
pre-treatment dens.	20	2.74	0.0979
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	25.91	<.0001
0 vs. 24	20	37.93	<.0001
4 vs. 24	20	1.27	0.2597

Control, 08.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.40	0.6511
pre-treatment dens.	20	0.10	0.7571
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.46	0.4956
0 vs. 24	20	0.57	0.4486
4 vs. 24	20	0.00	0.9684

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.64	0.5247
pre-treatment dens.	20	0.00	0.9474
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	0.00	0.9852
0 vs. 24	20	1.00	0.3163
4 vs. 24	20	0.90	0.3422

Drift, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	8.83	0.0003
pre-treatment dens.	20	7.02	0.0081
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	11.30	0.0008
0 vs. 24	20	11.13	0.0008
4 vs. 24	20	0.06	0.8078

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	0.98	0.3765
pre-treatment dens.	20	0.02	0.8870
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	1.14	0.2866
0 vs. 24	20	0.06	0.7995
4 vs. 24	20	1.75	0.1862

Control, 16.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	2.83	0.0645
pre-treatment dens.	20	1.96	0.1619
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	4.41	0.0357
0 vs. 24	20	2.33	0.1270
4 vs. 24	20	0.80	0.3722

Tab. A4 (continued).

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	7.96	0.0004
pre-treatment dens.	20	0.07	0.7950
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	11.56	0.0007
0 vs. 24	20	12.91	0.0003
4 vs. 24	20	0.04	0.8372

Drift, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	3.75	0.0285
pre-treatment dens.	20	1.10	0.2939
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	2.03	0.1547
0 vs. 24	20	6.61	0.0101
4 vs. 24	20	2.05	0.1524

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	21.83	<0.0001
pre-treatment dens.	20	0.79	0.3731
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	17.42	<.0001
0 vs. 24	20	42.05	<.0001
4 vs. 24	20	5.63	0.0177

Control, 23.07.03	Type III test of fixed effects		
effect	df	F	p
distance	20	6.39	0.0024
pre-treatment dens.	20	3.43	0.0642
contrasts	AnovaF		
	df	F	p
0 vs. 4	20	6.79	0.0092
0 vs. 24	20	9.87	0.0017
4 vs. 24	20	0.21	0.6471

9.2 Publikationen

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Langhof M., Meyhöfer R., Poehling H.-M., Gathmann A. 2005. Measuring the field dispersal of *Aphidius colemani* (Hymenoptera: Braconidae). Agriculture, Ecosystems and Environment, im Druck.

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